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AN INTRODUCTION
TO
THE STUDY OF RECENT CORALS

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AN INTRODUCTION TO THE STUDY OF RECENT CORALS

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PREFACE

WHEN a naturalist has the good fortune to spend a few weeks or months within easy reach of a tropical coral reef he gains an impression of animal and vegetable life which he can never forget. It may be that his aesthetic sense is, at first, stimulated and charmed by the beauty of shape and colour that he sees, but his more permanent interest becomes diverted to the intricate correlations of the multitude of living organisms and the infinite variety of their form and structure.

From the time of such an experience everything which is brought to him from a coral reef by friends and seamen is not only an object of interest, but often brings with it a thrill of reminiscent pleasure. It is difficult for him to shake off, if he desired to do so, the fascination of the corals.

Since my visit to the coral reefs of North Celebes many years ago I have received from several friends specimens from the shores which they have explored, not only the hard stony things called corals, but soft glutinous things, animal and vegetable, fish, and some worms and sponges. I wish I could find time and patience to describe the many points of interest in all these things, but I must confine myself within certain limits, and these must be the boundaries, wide as they are, of my own conception of the meaning of the word "coral." But if I write about corals I cannot limit myself to those of the coral reefs, for such things are not restricted, as many may suppose, to the warm tropical seas but are, as will be seen in the text, world-wide in their distribution.

The immense numbers of genera and species of recent

corals which have been brought to light render the task of compiling a complete systematic treatise on them a work of such gigantic proportions that it is beyond the powers of a single naturalist to complete it. All that has been attempted, therefore, in this book is to place before the reader a short description of a few illustrative genera of each of the groups of animals and plants which form coralline structures, to be a handy introduction to his studies and to help him to distinguish the corals belonging to the different groups.

It is difficult for students at home, who have only the hard skeletal parts to handle, to realise that in their natural haunts the corals are living, breathing, and feeding animals or plants, and no study can be complete or satisfactory unless some knowledge can be gained of the structures by which they capture and digest their food, the colours they display in life, and the means by which they propagate their kind. A short account of the soft parts of the coral and of their appearance when alive are therefore included, wherever possible, in the description of the genera.

The accurate determination of corals is not only of importance for the student of pure science, but it has its economic value in the study of the problems of distribution and variation of the coral reefs of the world. It may be suggested that the sea-charts and marine surveys would be more valuable than they are if some description were given of the kind of coral of which dangerous reefs or shoals are composed. If this little book will help mariners to identify such corals it may serve a useful purpose.

I regret very much that I have not been able to include in the text any reference to fossil corals. The story of the evolution of corals is of extraordinary interest, and the part played by them in building up many of the geological strata is of the greatest importance. A book dealing with this subject is greatly needed, but it should be a sequel to rather than a part of such a book as is now presented to the public.

In compiling the text I have had to consult many of my colleagues in the different Faculties of the University. I wish to acknowledge with gratitude their willing and valuable

assistance. The last chapter on the history of the trade in coral could not have been written without the help of several of my classical friends. I am also indebted to Sir Thomas Arnold, Professor Pelliot, and Professor Parker for references to coral in Arabic and Chinese literature.

Nearly all the illustrations are new, and have been prepared by the Lyth Engraving Company from photographs of specimens in the Manchester Museum or from drawings by Miss D. Davison. Some of the photographs were taken by Mr. J. T. Wadsworth of the Zoological Department, and by Mr. J. W. Jackson and Mr. H. Britten of the Manchester Museum. To Professor W. C. McIntosh, F.R.S., I am indebted for the fine specimen of *Filograna implexa* illustrated on p. 194.

S. J. HICKSON.

28th June 1924.

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CHAPTER I

ON THE USE OF SOME WORDS

“ A truly wise Man is so fully sensible how little he knows and what Things he once was ignorant of, which he is now acquainted with, that he is far enough from supposing his own Judgment a Standard of the Reality of things.”—HENRY BAKER, *An Attempt towards a Natural History of the Polype*, p. 216. 1743.

THE origin of the word Coral is one of those things about which we are still in doubt. The English form of the word is of course derived from the Greek *κοράλλιον* or its Italian equivalent *Corallium*, and according to various authors the Greek form was derived from *χειράλιον*=what becomes hard in the hand, or *κόρη* and *ἄλος*=the maiden or nymph of the sea, or *κῆρ* and *ἄλος*=the heart of the sea (with reference to its colour).

But all these hypotheses as to the derivation of the ancient Greek word seem to rest on very slender foundations.

It has been suggested by Reinach¹ that the word was of Celtic origin, and this suggestion is quite consistent with a more general view, which it is perhaps safest to adopt, that it was incorporated into the Greek language from the tongue of some wilder race of European nomads, who used it for ornamenting their weapons in prehistoric times.

What is certain, however, is that it was used in the early days exclusively as the name of the substance which is now called Precious coral, the *Corallium nobile* of the Mediterranean Sea, the axis of which has been used from very ancient times as a jewel or charm.

¹ S. Reinach, *Revue Celtique*, xx., 1899.

The derivation of the word from *χειράλιον* was probably suggested by the belief of the ancients that the Precious coral is soft in the sea and hardens when exposed to the air.

Sic et Corallium, quo primum contigit auras
tempore, durescit ; mollis fuit herba sub undis.

Ovid, *Metam.* xv. 416-7.

This idea prevailed for a great many centuries, and it is not clear who was the first to prove its error ; but Imperato writing in 1699 denied its accuracy, and even before that time Nicolay¹ had assured himself that the axis was hard in the water by making the sailors plunge their hands into the sea to test it before the coral was brought on deck.

In the sixteenth and seventeenth centuries we find the word Coral applied to other things than the Precious coral, thus Gesner (1565) called the coral now known as *Oculina Corallium verrucosum*, and Lobel (1575) the coral now known as *Dendrophyllia Coralloides sive Corallii varietas*. Imperato applied the name *Corallium album* to examples of several white corals, but also introduced the name *Porus matronalis ramosus*, from which the generic name Madrepora has been derived for *Dendrophyllia*, and the word Millepora for the coral now known as *Caryophyllia*.

From that time onwards the word *Corallium* and the modernised forms of it, Coral, Corail, Koralle, Corallo, etc., have been applied to such a variety of animal and vegetable marine organisms that it has lost its original restricted meaning. It is difficult, therefore, to give a definition of the term Coral that would satisfy at the same time modern usage and historical research. But some kind of definition must be attempted in order to indicate the scope of the present work, and in making this attempt I shall endeavour to convey the meaning that the word has acquired.

It is clear from what has already been said that the Precious coral of commerce must be included in the definition, and it is also clear that the large white Madreporæ

¹ Nicolas de Nicolay, who is described as the "valet de chambre et géographe ordinaire" to the King of France, was sent in 1551 to the coast of Algiers to investigate and report upon the coral fisheries of that region (Masson).

and Brain corals of the Coral reefs cannot be left out. All these things are undoubtedly members of the Animal Kingdom and belong to the group of animals known as the Coelenterata.

Moreover, if I were on a Coral reef with a few friends of good education but not of scientific tastes, and were to show them a Nullipore, they would in all probability call it a Coral, and I should regard myself as a pedant if I said, "No, it is a coralline alga," and the same if I denied that the pieces of Lithothamnion brought up in his trawl by the fisherman in the English Channel were corals, because they happen to be plants. To restrict the use of the word Coral to organisms or the products of organisms that are animals would be to change the meaning the word has acquired in everyday language, and *a fortiori* to restrict the use of the term to animals that belong to that subdivision of the Animal Kingdom called the Coelenterata would also be most undesirable and impracticable.¹

Nevertheless, the word as it is used by men of science and by the general public has some definite restrictions. It is not used for anything except certain animals and plants or the productions of animals and plants that live in sea-water or have lived in sea-water in prehistoric times. It is used principally for such animals and plants that produce a solid skeletal (or more accurately *shell*) structure of calcium carbonate which persists as such entire, after the death of the living organisms that produced it. The corals are, moreover, sedentary organisms, that is to say they are either fixed to some other hard substance at the bottom of the sea, or, if free, are incapable of moving about from place to place.

According to this definition, therefore, the things included in the term Corals are the calcareous marine plants, certain Foraminifera and Sponges, the Madreporarian corals, certain Alcyonaria (such as the Precious coral), and Hydrozoa, and also some genera belonging to the Polyzoa and Annelida.

¹ CORAL—A hard calcareous substance consisting of the continuous skeleton secreted by many tribes of coelenterate polyps for their support and habitation (Murray's *New English Dictionary*).

It is a word, in fact, which has no longer any defined meaning in zoological and botanical systematics, but signifies simply a heterogeneous group of organisms or the products of such organisms that have the common habit of living in the sea and producing a *shell* structure of carbonate of lime.

Such a definition, or rather attempt at a definition, is incomplete without reference to some special cases. There is a certain group of animals, known to the zoologists as the Antipatharia, which produce a hard black axial structure of keratin or horn, and the substance of this structure can be polished and used in the same way as the Precious coral. It was used by the ancient Greeks as an antidote (*ἀντιπαθής*) to poison, it was called by many writers of the sixteenth and seventeenth centuries the *Corallium nigrum*, and is still called Black coral in the shops where it is sold. Some reference to the Antipatharia, therefore, should be made in any general account of Corals, although they do not secrete any calcium carbonate and are not included in the general definition of the word.

The large subdivision of the Animal Kingdom called the Mollusca, and also the Brachiopoda, include many forms that are sedentary in habit and secrete shells of calcium carbonate, but all of these must be excluded from the definition, for I do not believe that the name Coral has ever been applied to them by serious students of Natural History.

A more difficult question to decide is whether to include in a general treatise on Corals, the Alcyonaria with hard axes of horny substance or with axes composed of both horny and calcareous substance which have been known for a long time under the general name of "Gorgonia." There can be no doubt whatever as to their close zoological relationship with the Precious coral, and one genus of them, namely *Isis*, was known to Imperato as *Corallium articulatum* and to later writers as the "King Coral" or "Jointed Coral." On the other hand, they are also closely related to the soft and spongy Alcyoniums (Dead Men's Fingers) of our own coasts and the Sarcophytums of the coral reefs which were not usually given the name Coral by the older writers.¹

¹ See, however, Milne-Edwards on p. 6.

There are a few Alcyonaria such as the Blue coral (*Helipora*), the Organ-pipe coral (*Tubipora*), the Precious coral (*Corallium*), and some others that are less known which must still be classed with Corals on the ground that they form compact shell structures of calcium carbonate that do not disintegrate into isolated spicules on maceration in sea-water; but in my opinion many of the Alcyonaria should not be called Corals.

The large and heterogeneous group of organisms which were formerly known as Corallines, also presents us with many difficulties. Some of these, such as the Polyzoan genus *Cellepora*, formerly classed with the "Cell-corallines," cannot be omitted from a general treatise on Corals, but the majority of the Polyzoa and also Hydrozoa with chitinous or horny tests, such as the Pipe corallines (*Tubularia*) and the Herring-bone or Vesicular corallines (*Sertularia*, etc.), are not corals in the usual meaning of the word.

It will be seen from this attempt to define the word "Coral" that it is a word of very ancient origin which, from having a very restricted application to one kind of marine product, has gradually acquired in the course of the ages a vague and ill-defined meaning. It conveys now to the mind not a definite species of the Animal Kingdom but a strange assortment of marine organisms both animal and vegetable, which make a hard calcareous, or in some cases horny, structure that resists disintegration after the death of the living tissues.

No attempt to restrict its use to its original meaning, and to invent such terms as "false corals" or "coralloids" or "pseudo-corals" to everything of this nature except the species of the genus *Corallium* as it is now used, could possibly be accepted. It would lead to such absurdities of language that you might search the coral reefs of the world and not find a single species of the true coral. It would necessitate the alteration of many thousands of labels in the museums and would create confusion in our literature.

The difficulty of defining a word such as Coral, that has come into popular use and has reference to things that are not fully understood even by those who have made a pro-

longed study of them is, as a matter of fact, insuperable. And it is the same with many other zoological words and expressions, because, as we become better acquainted with the vast number of species and varieties of animals and plants which exist in the world, the more clearly do we realise that our systems of classification and the frontiers we establish between one group and another are artificial and unnatural. If we knew all that could be known about animals living and extinct we should find that there are no boundaries separating one group from another, but a continuous series of forms showing tendencies to a great increase in numbers in certain parts of its course or in certain periods of time.

It is not surprising, therefore, that as our knowledge expands our system of groups is changed, and with the change there comes inevitably an alteration in the meaning of words. Such a change of meaning in the word Coral has taken place during the sixty-five years that have elapsed since (in 1857) Milne-Edwards published the important treatise entitled *Histoire naturelle des coralliaires ou polypes proprement dits*. In this great work the class of the *Coralliaires* was defined as "Radially symmetrical animals with the following characters: (1) A centrally placed mouth surrounded by tentacles and no true anus; (2) the body provided with a single system of cavities of which all parts communicate freely with one another and with the exterior; and (3) the organs of generation are situated in the general cavity of the body." With this definition of the *Coralliaires* the distinguished French author included in the treatise not only the Alcyonaria and Zoantharia that form coralline structures of calcium carbonate, but also the whole group of the Sea-anemones, the spongy Alcyonidae, the Order of the Sea-pens (Pennatulacea), and several other forms that are not, at the present day, usually called Corals. On the other hand he excluded from his treatise all the coralline Algae, Protozoa, and Polyzoa, and if he had been in possession of the knowledge we have gained since his time he would also have excluded, on the strength of his definition, such important corals as Millepora and the Stylasterina.

The word "polype" used in the sub-title of his work needs a few words of comment at this stage, as it also has changed its meaning to some extent.

The Greek word *πολύπους* (Latin *polypus*) or "many-footed," was applied by Aristotle and other ancient writers to the cuttlefish or octopus, and from this word was derived the French word "poulpe," signifying a cuttlefish. When the naturalists of the eighteenth century examined the living corals and saw emerging from the outer crust a number of small animals of tubular form, with a mouth at the free extremity surrounded by a circlet of tentacles, they were reminded of the cuttlefishes and octopuses with which they were well acquainted.

Thus Peyssonnel, writing about the Precious coral, said that he had discovered that "la fleur de cette prétendue plante n'était au vrai, qu'un insecte semblable à une petite ortie (*i.e.* sea-anemone) ou poulpe." And Trembley, in the account of his remarkable observations on Hydra, refers to it as the "polype d'eau douce." The great French entomologist Réaumur, however, who, assisted by Bernard de Jussieu, repeated Trembley's experiments on Hydra, must be held responsible for the establishment of the name polype for these animals because "leurs cornes sont analogues aux bras de l'animal de mer qui est en possession de ce nom" (*i.e.* poulpe).

When later observations showed that the polyps of the Hydrozoa differed in structure from the polyps of the Anthozoa and these in their turn from the polyps of the Polyzoa, an attempt was made to restrict the use of the term to the polyps of the Anthozoa. Milne-Edwards, however, protested against this restriction as being prejudicial to the interests of science, and said that the word could be usefully maintained for the soft and contractile parts of the Polyzoa, the Hydrozoa, the Alcyonaria, and the Zoantharia, and should not be employed for one or more zoological groups to the exclusion of others.

In modern times the word polyp has still a vague and ill-defined meaning. It is applied to the isolated fresh-water Hydra and to the animals that construct the horny

and calcareous structures of the Hydrozoa, Zoantharia, and Alcyonaria. In the group of the Polyzoa the derivative word "polypide" is usually employed for those parts of the body of the animals that are capable of extension and retraction, and the word polyp is rarely used with reference to the solitary sea-anemones.

In the case of several Hydrozoa and some of the Alcyonaria the animals that build up the structure of a single colony are found to be of two or three different kinds, performing different functions in the economy of the colony as a whole. In these cases great confusion has arisen as to the use of the word polyp.

Thus Köl liker suggested that in the dimorphic Alcyonaria the word polyp should be restricted to those individuals of a colony that exhibit the full number of tentacles and mesenteries, and the word "zoid" employed for those individuals in which the tentacles and mesenteries are reduced in number or absent. This proposal is obviously inconvenient, although it has been constantly maintained by the German writers, because it suggests a homological difference between the two kinds of animals of such a colony which does not exist. It would be better to use some prefix to the word polyp, such as auto- and siphono-, to indicate the difference in structure. But this has not been done. Another word has been introduced which lends itself more readily and euphoniously to the use of prefixes, and instead of auto-polyp and siphono-polyp, for example, the words auto-zoid and siphono-zoid are employed. The word "zoid" then may be regarded as a synonym of the word "polyp," but, whereas the latter is used only in a general sense, the former may be used with a prefix to signify a particular kind of polyp or zoid.

Thus, in speaking of the Precious coral, it may be said that the colony is formed by a number of polyps, and that these polyps are of two kinds, which are called the auto-zoids and the siphonozoids respectively.

The word polyp has thus come to be used in very much the same sense as Milne-Edwards used it in the sub-title of his book, "polypes proprement dits," but the word coral

has become extended in its meaning to include living structures, such as certain Foraminifera, Sponges, and the coral-line Algae for example, that possess no such organised animal forms as could be, by any possibility, included in the meaning of the word polyp. There can be no longer, therefore, any synonymy between the words "Coral" and "Polyp."

Another word which must be frequently used in a book on Corals is the word "Individual," and this is as difficult or even more difficult to define than any of the others. Many attempts have been made by eminent philosophers, such as Huxley, Bergson, and others, to give a scientific definition of it, but each one seems to lead to absurdities or to a use of the word in a sense that it is not used and cannot be used in common language. To give just two examples to illustrate my meaning. If we were to accept Huxley's definition of the word individual as "the total product of a fertilised ovum," we must regard the winged insect, the Aphis, which we find on our rose trees, not as an individual but as the millionth (or more) part of an individual. Or if we follow Bergson's analysis of the word, then we are led to the conclusion that the Yucca plant and the Pronuba moth, which are known to be mutually dependent on each other for continued existence, are not two individuals but one individual of the fifth or sixth order of individuality.

In my opinion the only definition of the word that can bring it into agreement with its usage in modern language in biology is one which expresses the discontinuity of an organism in time and space.

In the case of an isolated polyp such as a hydra or a sea-anemone, there is no difficulty in grasping the idea of the individual, and, if the hydra is reproducing by gemmation, the bud that is not yet detached from the body wall is a part of the individual hydra. When the bud has developed tentacles, and has lost organic continuity with the parent hydra, it becomes a separate individual. The idea of separate individuality in this case is dependent on the discontinuity in space.

In the genus *Diaseris* there is a single free individual polyp which secretes a large fungiform calcareous structure.

When it has reached a certain size or under certain unknown environmental conditions, it breaks up into four segments, and each of these four segments continues to live independently and in time restores the symmetrical shape of its parent. In this case the single individual *Diaseris* has given rise to four individual Corals of the genus.

An *Alcyonium*, a *Tubipora*, or a *Madrepora* is an organism consisting of a number of polyps in organic continuity and mutually dependent on one another for their continued existence.

Here again the *Alcyonium* or the *Tubipora* as a whole is, in common language, the individual, and the polyps part or organs of the individual. The conception of individuality has no relation to the structure or function of the parts but to the discontinuity of the living organism as a whole from other living organisms.

One difficulty, however, in the way of accepting this definition of the word individual is that the corals which are compound or formed of numbers of polyps in organic continuity are frequently called "colonial" corals, and it seems impossible to reconcile the conception of "colony" with that of "individual."

But the word colony was introduced into the science in error and is really a misnomer. It might be applied to the bees in a hive or to the ants in an ant-nest, for these insects, although congregated together for their mutual advantage, are individually free, and it was due to the error of Réaumur and others of his time, who regarded the calcareous structure of corals as formed in the same way as bees or wasps construct their combs, that the expression "coral insects" came into use and the conception of colony formation was introduced.

As the English-speaking people become accustomed to the use of the word "polyp" the expression "coral insect" may disappear from our language, but it will be more difficult to eradicate the use of the word colony as applied to these animals, because there is no other word in our language which can be readily substituted for it.

"Zoophyte" is another word which was formerly applied

to many of the corals and other living organisms which have a plant-like form or method of growth. According to Milne-Edwards the first record of its use in this sense is to be found in an edition of the writings of Elien by P. Gyllius, 1535, in which these words occur, "Plinius urticam et spongiam numerat inter ζωόφυτα." Whatever may have been the more restricted application of the meaning of the term in the days of the classical writers, we find it applied in the eighteenth century to all the Corals, Hydroids, Gorgonians, Polyzoa, coral Algae, and even to some of the Protozoa (*e.g.* Vorticella) and Rotifera (*e.g.* Brachionus). The general idea underlying the use of the term was that these things were neither wholly animal nor wholly vegetable in nature but in some respects animal and in other respects vegetable.

In this connexion a view expressed by Rumphius is of some interest. He gives a description of a marine product which he found at Amboyna (probably a Cavernularia) called the "Phallus marinus," and, in describing its position in the classes, says that in the element of the water there are things which are hardly animals or plants but seem to be the relics of primordial chaos, and among these there are living, growing, and mineral things, such as plants which are alive, stars which grow, and animals which resemble plants.¹

Pallas² was of opinion that Nature connects together even the most different things and thus has brought together the Animal and Vegetable Kingdoms in the form of the Zoophyta, for these things combine the nature of animals with the nature and form of plants.

In the middle of the eighteenth century, however, the current views of the nature of the Zoophytes were shaken by the publication of the remarkable observations and experiments of Trembly on the freshwater Hydra and of Ellis on certain Hydroids at "Brighthelmstone in Sussex" and on Alcyonaria at Whitstable. To Peyssonnel, however, must be given the credit of having been the first to

¹ See heading of Chapter III. p. 23.

² Pallas, *Elenchus zoophytorum*, Sections xv., xvi., xvii., xviii.

demonstrate by observation and experiment that these things are animals. Peyssonnel conducted his investigations on the Precious coral in the neighbourhood of Marseilles in 1724 and 1725, and wrote an account of them in which he clearly expressed his view as to the purely animal nature of the Coral polyp.

But the views of the leading authorities of the French Academy, and particularly of Réaumur, were so firmly fixed that it was considered to be an act of charity to Peyssonnel to refuse to publish his revolutionary opinions, and even when he sent a communication on the subject in 1753 to the Royal Society of London, which was published three years later, the name of the author was suppressed. Fortunately Peyssonnel's manuscripts were preserved in the library of the Natural History Museum in Paris and due credit has since been given to him for his discoveries.

Ellis,¹ whose work was certainly done without knowledge of what Peyssonnel had written, expresses his opinion very clearly in the following sentence: "I own I am led to suspect that by much the greatest part of those Substances, which from their Figure have hitherto been reputed Sea Shrubs, Plants, Mosses, etc., are not only the Residence of Animals, but their Fabric likewise; and serve for the Purposes of Subsistence, Defence and Propagation, as much as the Combs and Cells fabricated by Bees, and other Insects, serve for similar Purposes."

The result of these investigations was that Linnaeus removed the Zoophytes from the Vegetable to the Animal Kingdom, where they have remained ever since, but in doing so he retained a modified form of the older view as to the dual nature of these organisms.

It is not quite clear what Linnaeus really believed about the Zoophytes, but judging from the brief statements he gives in Latin he thought that the stem is vegetable but becomes metamorphosed into animal when it flowers—

stirps vegetans, metamorphosi transiens in florens Animal.

¹ J. Ellis, *Natural History of the Corallines*, p. 100. 1755.

"The Zoophytes are not, like the Lithophytes, the producers of their shells or trunks but the shells of themselves ; for the stems are true plants which, being metamorphosed, change into animated flowers (true animalculae) completed by organs of generation and instruments of motion, in order that they may obtain motion which extrinsically they have not got."

The Lithophytes of Linnaeus consisted of the genera Tubipora, Madrepora, Millepora, and Cellepora, and he seems to have regarded them as entirely animal in nature.¹

Linnaeus was the last of the great naturalists of the eighteenth century to cling to the view that the Zoophytes are wholly or in part of a vegetable nature.

But John Ellis,² one of the most brilliant and observant naturalists of his time, who expressed most emphatically the view that the Zoophytes are entirely animal in nature, was led into the error of asserting that certain calcareous Algae which he had studied are also produced by animal organisms. Influenced perhaps by a statement made by Linnaeus that all calcareous substances must truly be of animal production, he included in the Animal Kingdom the Corallines which are now called Lithothamnion, Amphiroa, Corallina, Halimeda, etc. (see Chap. X. p. 197).

In justice to him, however, it is only fair to quote a passage which shows that he held this view with some misgiving.

"What and where the link is that unites the animal and vegetable kingdoms of nature no one has yet been able to trace out ; but some of these corallines appear to come the nearest to it of anything that has occurred to me in all my researches ; but then the calcareous covering, though ever so thin, shows us that they cannot be vegetables."

It is not surprising that, as a result of the researches of Peyssonnel, Ellis, and others, the word zoophyte gradually fell into disuse. De Lamarck (1816) said : "It is not at all convenient to give to Polyps the name Zoophytes because

¹ Animalia Mollusca, composita Corallium calcareum, fixum, quod inaedificarunt animalia affixa (*Systema Naturae*, xii. ed. i. pt. 2, p. 1287).

² J. Ellis, *Phil. Trans. Roy. Soc.*, 1767.

they are solely and completely animals, for their body is no more vegetative than that of an insect or any other animal."

The fate of the word, however, was not sealed until, by the researches of Tozzetti and subsequent authors, the Nullipores were proved to be "*uniquement et complètement*" vegetative, and the position was then reached, which may be safely regarded as final, that some Zoophytes are animals and some are plants, but there are none which partake of a dual nature, being animal in some respects and plants in others.

But is it necessary that this word should entirely disappear from our literature? Perhaps not. If it is used collectively to signify that strange assortment of animals belonging to several distinct orders of the Animal Kingdom which have a plant-like habit and method of growth, it has a place in our vocabulary which is not otherwise provided for.

CHAPTER II

ON THE STRUCTURE AND CLASSIFICATION OF CORALS

“ Il n’y a dans le Corail ny fleurs, ny feuilles, ny chair, ny graine, ny racine et cela posé, je crois qu’il est bien éloigné du genre des plantes.”—BoccONE, 1674.

THE large and very heterogeneous assembly of organisms forming the calcareous or horny structures which are commonly called Corals may be divided into two great divisions : the Animal corals and the Plant corals.

The Animal corals may be again divided into two groups, namely, those that bear polyps and those that do not bear polyps ; and the Plant corals also into two groups, the Red Seaweed corals and the Green Seaweed corals.

The polyp-bearing corals must be subdivided into a number of orders according to the anatomical characters presented by the polyps, but before this further subdivision can be made clear to the reader it is necessary to refer very briefly to essential characters presented by these animals.

There can be no doubt that when the word poulpe or polyp was first introduced in this connexion the important differences between different kinds of polyps, which more modern researches have revealed, were not understood nor even suspected.

The word has no precise zoological meaning in modern literature, but still retains its utility when applied to animals which present certain superficial external characters in common. It is not a word for which we can find a rigid definition, and the student of zoology must be prepared to

find many examples of organisms which may or may not be called polyps according to the inclination of different authors.

But in general terms a polyp is an animal which is sedentary in habit and more or less cylindrical in shape, which possesses a mouth, surrounded by a crown of tentacles, and an alimentary canal or a body cavity in which food is digested.

There are many polyps which are solitary, but more generally they build up, by budding or by division, colonies of polyps in organic continuity with one another. If we

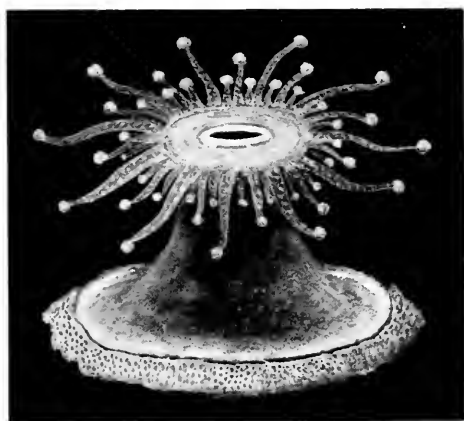


FIG. 1.—A fully expanded *Caryophyllia* polyp, showing the slit-like mouth in the centre and the ring of capitate tentacles surrounding the oral disc. (After de Lacaze-Duthiers.) $\times 14$.

take an example of a solitary polyp, the coral *Caryophyllia* (Fig. 1), we can see, when it is fully expanded, that it possesses a mouth placed in the centre of a disc surrounded by a single ring of tentacles. In a colony of polyps, as is shown in the diagram of an Alcyonarian (Fig. 44), we see a number of polyps connected together in a common fleshy substance (the coenenchym) by a system of canals (coenosarcal canals). Sometimes we find that the polyps in such a colony are all alike in structure; in other cases we find they are of two kinds, as in the diagram, when they are called dimorphic colonies. In the dimorphic colonies the two kinds of polyps perform different physiological functions and show different structural characters in adaptation to the performance of those functions. In such cases the word zooid is used instead of polyp, with a prefix to indicate in some way the functions it performs (*e.g.* Autozooid and Siphonozooid in Fig. 44).

The reasons for calling the polyps Animals can now be

explained. The tentacles are organs for catching and in some cases killing or paralysing the food which passes within their reach in the surrounding water, and the food is passed through the mouth into a cavity where it is digested. The food consists of various floating or drifting micro-organisms, mostly animal in nature, so that this method of feeding is similar to that of other animals or, as it is called in technical language, *holozoic*.¹

The polyps also possess the power of movement. It is true that they cannot move from place to place in search of their food as the higher animals do, but they are provided with bands of muscles which enable them to expand and retract their bodies. They are sensitive and irritable, responding by muscular movements to stimuli of light, heat, and chemical change in the surroundings.

They produce in a season of the year eggs and sperms, and the eggs when fertilised give rise to ciliated larvae which swim away and develop into a new polyp or colony of polyps. All these characters, combined with features of more minute structural anatomy which it is not necessary to describe in detail, prove that the polyps are solely and completely animal in nature.

Some of the polyp-bearing corals possess an additional character which Linnaeus considered to be also an attribute of animal life only, but which we now know may also occur in plants, that is, the secretion of calcium carbonate.

The calcium carbonate is secreted in various ways in different kinds of corals, but there is this in common to all of them, that it is always secreted by cells of the outer layer of the body—the ectoderm—and is therefore, strictly speaking, an outside support or exoskeleton, although in some corals it becomes deep-seated and internal by subsequent changes in its relation to the soft parts.

The calcium carbonate which is secreted by the ectoderm cells solidifies to form the complex calcareous structures of such varied shape and structure with which we are familiar in our museum collections as the "Corals." The word

¹ For a further note on the nutrition of corals, see p. 20.

Coral, however, being generally used in a very indefinite way, may mean in our common language either the dried calcareous skeletal structure alone or the whole living organism with hard skeleton and fleshy organs complete. It is therefore necessary to use the term "Corallum" when we desire to refer to the calcareous structures only, in contrast to the soft fleshy tissues that give rise to them.

To return to our system of classification.

The polyp-bearing corals belong to two widely separated divisions (*i.e.* Phyla) of the Animal Kingdom, called the Coelenterata and the Polyzoa.

It is not necessary to relate in detail the many anatomical and embryological differences between these two Phyla, for which reference should be made to one of the many good text-books of General Zoology. But there are two essential points to which attention may be called.

In the Coelenterata the mouth leads into a large undivided cavity in which the food is digested, and the indigestible parts of the food are ejected by the same aperture. In the Polyzoa the mouth leads into a stomach and intestine, and the indigestible parts of the food are ejected by an anal aperture which is quite distinct from it (Fig. 74, p. 158). There is thus a complete alimentary canal in the Polyzoa which is without any direct communication with the body cavity surrounding it.

In all the Coelenterata without exception the tentacles are provided with remarkable vesicles of microscopic size called "Nematocysts," and these have the power of inflicting a sting which kills or paralyses small animals that pass by and captures them by means of a thread that is discharged at the same time.¹ The Coelenterata are therefore animals that capture their prey by stinging them, and hence the name Cnidaria (from *κνίδη*=a nettle) is sometimes applied to them.

In a few corals (*e.g.* *Millepora*) the nematocysts are powerful enough to penetrate the human skin, causing a painful form of nettle-rash, but as a general rule living corals can be handled freely without any ill effects.

¹ See Fig. 69 on p. 148.

The Polyzoa never possess nematocysts. Their food is obtained by the action of currents of water produced by the ciliary action of the cells that cover the tentacles.

Of the animal corals that do not bear polyps there are only two groups, and neither of these have many representatives.

The living substance of the Foraminifera is not divided up into a number of cell units, but is a continuous mass or plexus of the vital stuff—protoplasm. There is no mouth, no body cavity, and no tentacles, but at the periphery the protoplasm spreads out into a complex web of filaments which can capture and digest small organisms that come in contact with it. The corallum is formed of a number of adjacent chambers which are perforated by an immense number of minute pores—the foramina.

There are only two or three sponges which can be called Poriferan corals, and these will be described in a later chapter. But, for comparison with other groups, it may be said here that the Porifera are multicellular animals—without any of the characters of polyps—which obtain their food by maintaining a constant flow of water through an elaborate system of canals and spaces in their body, certain cells of which have the power of catching and digesting such organisms as are nutritious.

The Plant corals all belong to that division of the Vegetable Kingdom which is known as the Algae. Most of the Algae with which we are familiar are soft and flexible, but two of the classes included in that division, namely, the Rhodophyceae or Red Seaweeds and the Chlorophyceae or Green Seaweeds, include genera which secrete a sufficient amount of calcareous matter to render them hard and resistant. As these coral Algae possess no mouths, holes, or cavities that can be seen except with a high power of the microscope, they were grouped together by the older writers under the common name of “Nullipores,” a name which has now generally fallen into disuse.

The classification of corals adopted in this book may be expressed in a tabular form as follows :

I. ANIMAL CORALS.

A. Polyp-bearing corals.

1. Coelenterate corals.

(a) Madreporarian corals.

(b) Alcyonarian corals.

(c) Antipatharian corals.

(d) Hydrozoan corals.

2. Polyzoan corals.

B. Corals that do not bear polyps.

1. Foraminiferan corals.

2. Poriferan corals.

II. PLANT CORALS.

A. Red Seaweed corals.

B. Green Seaweed corals.

ADDITIONAL NOTE ON THE NUTRITION OF CORALS

Although there can be no doubt that the polyp-bearing corals can catch and digest living organisms for food as described above, it seems to be highly probable that, in many cases, this food is not the only source of their nutrition.

The canal system and often the polyps themselves of many Coelenterate corals that live in shallow water are crowded with little spherical cells (*circa* 0.1 mm. in diameter) surrounded by a well-defined cell wall and bearing the characteristic coloured vegetable substance Chlorophyll.

These cells are not coelenterate cells belonging to the polyps but unicellular organisms, living under the protection of their hosts, with their own independent reproduction and nutrition. They should not be called parasites, for it is evident that they do not irritate or injure the polyps. They are of the nature rather of associates who live with the corals for mutual help and protection.

This kind of association is called symbiosis, and the unicellular organisms that take part in this symbiosis of corals are called the Zooxanthellae.

The great importance of these organisms in the general

physiology of corals cannot be fully estimated at present, as there are many points in the relationship between the symbionts that are in need of further investigation ; but some idea of the importance of the association may be conveyed by a brief statement of the facts that are known about a single example—the *Millepora* coral.

Millepora is a large massive or branching coral (see p. 145) which is found in shallow water all over the tropical world, and wherever it is found the superficial plexus of canals is always crowded with zooxanthellae.

No specimen has yet been examined either in the East Indies or the West Indies in which the zooxanthellae do not occur in abundance. It is not a case, therefore, of an infection confined to certain specimens or certain localities.

Moreover, it has been shown, in the case of *Millepora*, that there is no stage in the life-history of the coral in which it is free from this infection. The young egg cells in the ovary, long before they reach full size and maturity, are invaded by zooxanthellae from the surrounding tissues, and thus, when the egg is fertilised and develops into a larva, it is already provided with a full equipment of these symbiotic cells.¹

As no specimens of *Millepora* have yet been found without the zooxanthellae, we cannot tell if this coral can manage to exist without them, nor can we assert without experimental proof that the association is of any benefit to it.

But similar cases of symbiosis are known in other animals, and in one of these—the symbiosis of the little flat worm *Convoluta* with zoochlorellae—it has been shown experimentally that the *Convoluta* is dependent on substances formed by the zoochlorellae for at least an essential part of its nutrition.²

If, as seems highly probable, there is the same kind of relation between *Millepora* and its zooxanthellae as there is between *Convoluta* and its zoochlorellae, the holozoic method of nutrition of the coral is supplemented by the holophytic action of the chlorophyll-bearing zooxanthellae.

¹ J. Mangan, *Quart. Journ. Micr. Sci.* 52, 1909.

² Gamble and Keeble, *Quart. Journ. Micr. Sci.* 51, 1907.

The occurrence of zooxanthellae in the tissues of Coelenterates of various kinds living in shallow waters is very widespread, and in some cases where they are present in unusual abundance the digestive organs of the polyps seem to be degenerating.¹

These facts and other considerations give strong support to the hypothesis that the zooxanthellae play an important part in the physiological processes of the reef corals.

The nutrition of the zooxanthellae is probably purely holophytic, that is to say, it is a synthetic process carried on by the action of chlorophyll in sunlight.

In order, therefore, that the action may be most effective, the zooxanthellae should tend to collect in the superficial canals, and they should be as free as possible from shadows cast by surrounding objects.

This may account for the fact that has been commented on by so many observers, that the coral polyps are usually contracted in the day-time, and also for the fact that when the digestive centres of the polyps are examined they are usually found to be devoid of food.

The process of nutrition of corals may therefore be continuous but alternating in character. In the day-time the polyps contract so as to give the sunlight free access to the zooxanthellae in the superficial canals, and in the night, when chlorophyll action must cease, the polyps expand, spread out their tentacles, and capture the animal food which is as necessary for their sustenance as the starch that is passed on to them by the zooxanthellae.

Whether this is the whole story of the nutrition of corals it is difficult to say. That branch of science which deals with the physiology of the lower animals is still in its infancy, and it may be that in the light of new investigations our views on the nutrition of corals may be profoundly modified ; still it is difficult to believe that the elaborate and highly differentiated organs that the coelenterate polyps possess does not indicate that animal food is an important, if not essential, part of their nourishment.

¹ Edith Pratt, *Quart. Journ. Micr. Sci.* 49, 1905.

CHAPTER III

MADREPORARIAN CORALS

“Doch de Natuur is in 't Element des waters zoo verwart, dat men dingen vind, die men qualyk tot een van deze trappen brengen kan, als of'er overblyfzels van den eersten Chaos in gebleven waren: want hier loopen levende, groeiende en minerale dingen alle onder malkander, maakende planten die leeven, starren die groeijen, en dieren die de planten nabootzen.” — RUMPHIUS, *Rariteitkamer*, Book I. chap. xxxviii., 1705.

WHEN the Dutch naturalist Rumphius, at the end of the seventeenth century, varied his remarkable investigations on the plants of the Malay Archipelago by a study of the corals at Amboyna and found it was difficult to determine to what order of things they belonged, he exclaimed that in the element of water there remains a survival of primordial chaos.

To the naturalist of the present day, when he undertakes the task of bringing into some kind of system the huge numbers and variable forms of the Madreporarian corals and the literature that deals with them, it may seem also that here is the presence of a chaos which, if not primordial, is at least as difficult to unravel.

The Madreporaria are sometimes called the “Stony” corals, but this popular name does not in the least help us to distinguish a Madreporarian from any other kind of coral. It is true that the dried corallum is hard and inflexible like a stone and that, with a few rare exceptions, it is white, but the same may be said of *Millepora* and many other corals which are not Madreporaria. The only character that distinguishes them from other corals is the calyx (the calcareous

cup in which the polyps rest), with its radial septa, and even this character is sometimes difficult to recognise or define.

The Order provides the bulk of the corals of the world at the present day. In variety of structure and in the number of genera and species the Madreporaria exceed all the other kinds of corals put together; and it is in consequence of this preponderance that some authors would confine the expression "true corals" to those of Madreporarian origin and confer some other designation such as "corallines" or "false corals" on corals of a different Order. Such a plan, however, is historically unsound and from a practical point of view inconvenient.

The Madreporarian corals may be arranged in various ways. In former times, when very little or nothing was known about the characters of the polyps, the classification was based entirely upon the characters of the corallum. It has been found, however, that such a classification leads to the grouping together of corals that are not closely related to one another, and, conversely, corals that are closely related are, in such a system, widely separated.

A sound scientific classification should be based on a knowledge of all the characters possessed by these animals in both their hard and soft parts. Such a classification will fluctuate as our knowledge, which is still very imperfect, increases, and in that respect may cause some inconvenience, but it is the only kind of classification that will express the true relationship of these corals to one another.

The more empirical systems of classification, based on the characters of the hard parts alone, have some general utility and educational value, because in most cases such characters are the only ones that are available for the student at home, and the study of such characters must form the introduction to this branch of science.

Proceeding on such a system, an examination of a good collection of dried Madreporarian corals, such as may be found in any large museum, shows that they may be arranged in two groups.

In one may be placed those that exhibit a large number

of cup-like depressions for the polyps, and in the other, those that consist of a single cup. The former are called "Colonial" corals and the latter "Solitary" corals.

If the corals are then examined with a magnifying glass it is found that, in some, the walls of the cups and other structures are porous, and in others they are solid. The former are called "Perforate" and the latter "Imperforate" corals.

These two methods of grouping, however, are not similar, for in both the solitary and in the colonial groups there are examples of perforate and imperforate corals.

An examination of the base of a branch that has been broken off a large corallum also shows that the tubes which lodge the polyps are in some cases divided by transverse partitions or "Tabulae," as in *Millepora* and *Heliopora*, and in other cases are not so divided, and thus we can speak of corals that are tabulate and corals that are not tabulate.

All of these characters of the corallum may be of importance in the description of the corals and in their classification into families and genera, but it has been found that no one of them affords a sufficiently trustworthy character for the arrangement of the corals into large groups which are intended to express genetic relationships.

For this purpose reference is made to the characters that are shown by the anemone-like polyps which construct the coralla, such as, the number and form of the tentacles, the arrangement of the mesenteries, and the methods of gemmation and fission. It seems probable that these characters have undergone less change in the course of evolution than the characters of the coralla, and that they are, therefore, more trustworthy guides to genetic affinities; but even these characters cannot alone serve the purpose of a sound classification unless taken in conjunction with the characters of the corallum.

In order that the student may become acquainted with certain technical terms that it is necessary to use in the description of the Madreporarian corals, it is best to examine, in the first place, the structure of a specimen

of a solitary imperforate coral. For this purpose the English cup-coral, *Caryophyllia smithii*, may be taken (Figs. 1, 2, 3, 4).

The wall of the cup, which is approximately circular in section, is called the "Theca," and passing radially inwards

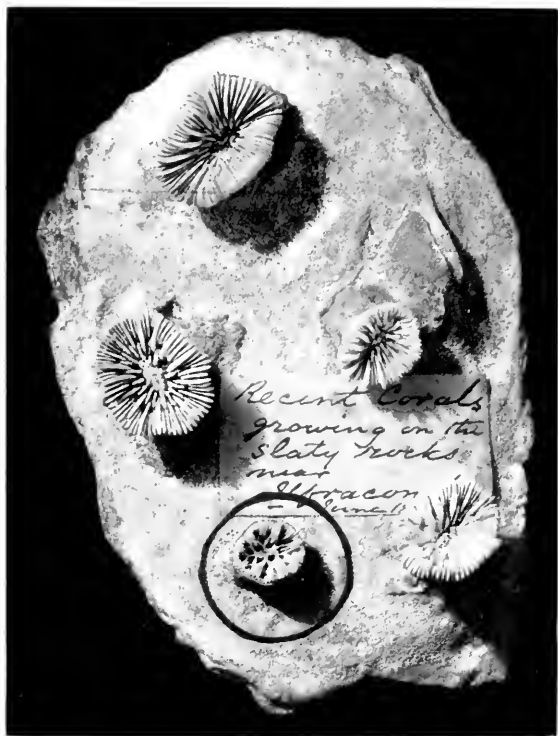


FIG. 2.—A group of four specimens of *Caryophyllia smithii* and one specimen (marked by a black ring) of *Balanophyllia regia* found at low water at Ilfracombe. Nat. size.

towards the centre of the cup are a number of vertical partitions which are known as the "Septa." From the centre of the bottom of the cup there rises up into the cavity a spongy dome-shaped calcareous mass formed of some ten to twenty thin twisted plates, called the "Columella." From the outer border of the columella a number of vertical plates similar to the septa, but more sinuous in

form, extend outwards radially, but do not reach the walls of the theca. These are the "Pali."

In the English cup-coral the septa are seen to project as crests a short distance above the rim of the theca, and are continued outside the rim as blunt ridges with granular edges, called the "Costae" or "ribs" (Fig. 4). Below the visible costae the outside of the theca is covered with a chalky deposit which extends outwards over the spreading base of attachment, and this chalky deposit is called the "Epitheca."

The polyp (see Fig. 1, p. 16) which forms this corallum is in appearance very much like a sea-anemone. In a

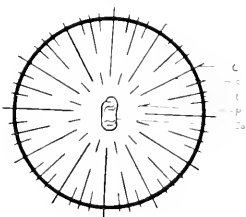


FIG. 3.—Diagram of a transverse section through the cup of a Caryophyllia. *C*, costa; *Co*, columella; *p*, palus; *s*, septum; *t*, thecal wall.

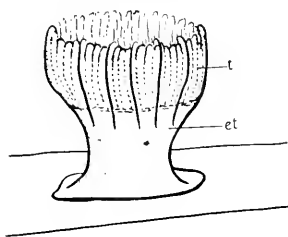


FIG. 4.—Diagram of an external view of a Caryophyllia to show the theca (*t*) with its projecting costae and the epitheca (*et*).

position corresponding with the centre of the cup there is a slit-shaped mouth surrounded by a flat disc. At the margin of the disc there are about fifty tentacles. Each tentacle is provided with a number of wart-like batteries of nematocysts and has a prominent white knobbed extremity, which is crowded with these stinging organs.

When the polyp is dissected it is found that the mouth leads into a short throat called the "Stomodaeum," and this communicates with the general body cavity. The stomodaeum is bound to the body wall by a number of vertical fleshy bands called the "Mesenteries," and consequently the appearance of a coral polyp in transverse section has a resemblance to a cart-wheel, the stomodaeum representing the hub and the mesenteries the spokes (Fig. 7,

p. 33). The number and arrangement of the mesenteries are important characters in classification.

The fleshy substance of which the polyp is composed is translucent and of a faint fawn colour, with a broad band of brown colour on the disc surrounding the mouth, and red or brown patches on the tentacles.

But, as in the sea-anemone, and, indeed, in most of the Madreporaria, the colours of the living polyps are so variable that the detailed descriptions of no two specimens from the same locality would agree. De Lacaze-Duthiers, in his description of some specimens from the coast of Brittany, states that in one of his specimens there was a circle of bright veronese green at the margin of the disc, and in others the walls were of brown or burnt sienna colour. In all varieties, however, the colour scheme is of exquisite beauty and of such delicacy of tone that it is almost impossible to interpret it justly by art.

As an example of a colonial and imperforate coral *Lophelia prolifera* (Fig. 5) may be taken. This coral, which is found in deep water in many localities off the western coasts of Europe, forms large tree-like growths with spreading and sometimes anastomosing branches. On each of these branches a number of cup-like prominences are arranged alternately right and left, which show a series of radiating septa like those of Caryophyllia. The prominences are called the "Calices," and the common substance which supports them is called the "Coenosteum."¹ A transverse section of the coenosteum shows a thick imperforate wall and an axial cavity divided into a number of chambers by radiating bands of coral substance which meet at a hub in the centre. Further investigations would show that these radiating bands are continuous with the septa of the calyx immediately above the section of the branch that has been examined, and that the branch has been formed by a process of budding and subsequent growth of a new

¹ Many writers on corals use the term "Coenenchym." This is etymologically and historically inaccurate. The word coenenchym was introduced by Milne-Edwards and Haime for the fleshy substance between the polyps in Alcyonaria (*Histoire naturelle des coralliaires*, 1857, vol. i. p. 29).

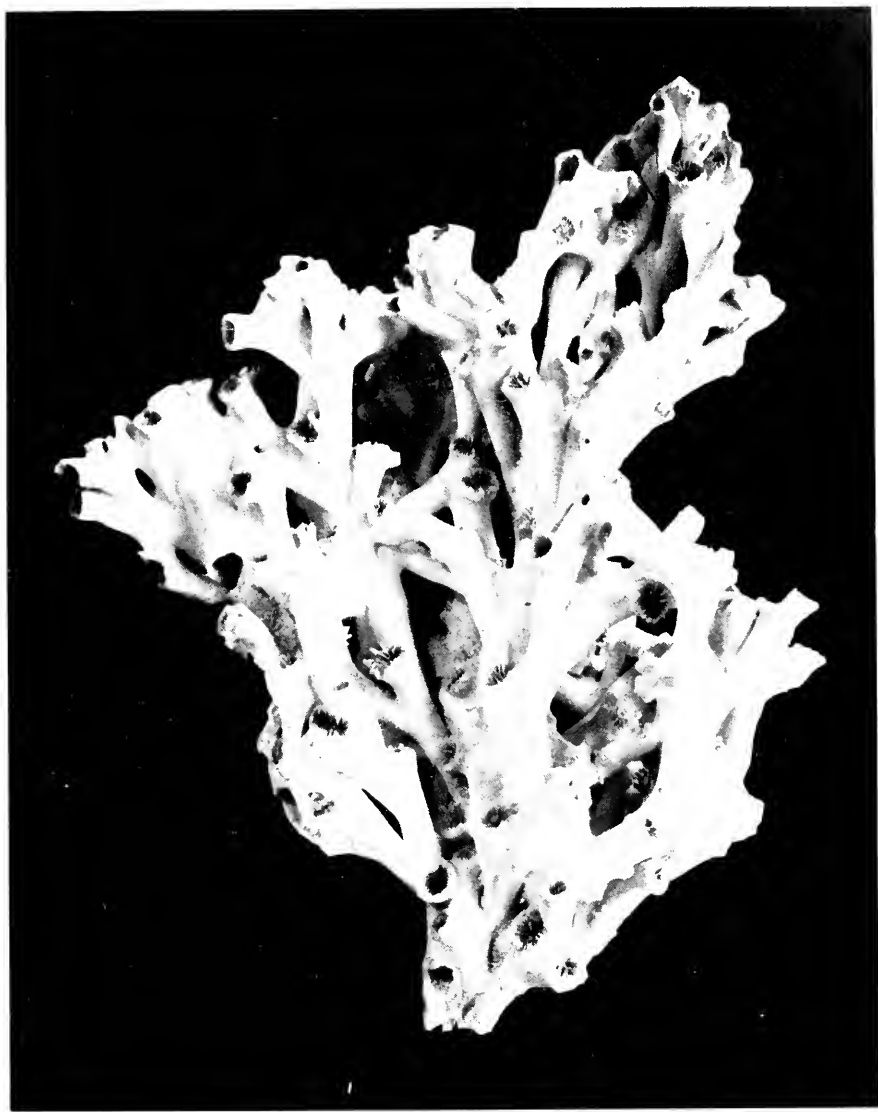


FIG. 5.—*Lophohelia prolifera* From the Bay of Biscay, 400 fathoms. $\frac{1}{2}$ nat. size.

polyp and calyx from the margin of the calyx of the youngest terminal calyx of the branch, followed in turn by the formation of a new polyp and calyx on the opposite margin of the former when it has reached a later stage of growth. This alternate right and left budding gives the younger branches of a large colony a curious zigzag appearance, but in the older branches the angles become smoothed out by the continuous growth of the coenosteum until they appear to be perfectly straight.

The study of this method of growth in *Lophohelia* is necessary in order to understand that the calyx of a coral corresponds with only a part of the corallum of a solitary coral like *Caryophyllia*. The lower part of the theca of the solitary coral is represented by that part of the branch which extends from the calyx to the level of the next calyx on the opposite branch. In other words, it might be said that this colony is formed by the coral polyps growing on one another's shoulders.

In other colonial corals it is not easy or not possible to demonstrate that the colony has been formed in this way, and consequently the coenosteum or matrix which bears the calices appears to be entirely communal in origin and function.

In another colonial imperforate coral, *Oculina*, for example, which is usually placed in the same family as *Amphihelia*, the calices do not project above the general surface of the coenosteum, and are not arranged alternately right and left, but seem to be arranged spirally or scattered about irregularly on all sides of the branches, and when the branch is examined in transverse section there is no axial series of chambers such as we find in the *Lophohelia* branch.

In the family *Astraeidae* or Star corals, which are usually placed next in order to the *Oculinidae*, the calices are more crowded together, so that the amount of coenosteum between them is reduced to small dimensions (*Galaxea*), or the calices come into such close juxtaposition that there is little or no coenosteum at all.

Before passing on to the complex forms of corallum produced by complete and incomplete fission or by perfora-

tion, reference may be made to the polyps of one of the colonial corals that has just been described and their relation to the corallum.

The polyps of *Lophohelia*, according to de Lacaze-Duthiers, are provided with a crown of tentacles of various lengths corresponding in number with the septa (about twenty in a full-grown polyp); the mouth in the centre of the disc is slit-shaped, the slit being parallel with the axis of the branch. The outer wall of the polyp flows over the rim of the calyx, and is continuous with a thin layer of fleshy substance that covers the coenosteum and brings the polyps into organic continuity with one another. This communal lining substance may be called "Coenosarc."

In life the polyps and the coenosarc are so remarkably transparent that the details of the coral structure can be seen through them, but nevertheless they do exhibit a faint yellow or orange colour, which is accentuated on the disc round the mouth. The tentacles are also transparent and faintly yellow in colour, dotted with little white spots, and terminating in a white conical point. All these soft parts of the *Lophohelia* colony are situated above the hard parts—there are no canals or other living tissues that penetrate into the coenosteum or into the septa or walls of the calices, and consequently, when the colony dies, the coenosarc peels off the coenosteum and the polyps become detached from their calices.

This is in marked contrast to what is found in perforate corals in which both polyps and coenosarc are firmly locked into the corallum by canals and strands of tissue that pass through the perforations.

The classification of the Madreporarian corals is still in a very unsatisfactory and unsettled condition, owing, in part, to the very limited knowledge we possess of the structure of the coral polyps, and in part to the wide range of structure that the group exhibits leading to interdigitation of the families and sub-orders.

In some of the Madreporaria, such as the genera *Madrepora* itself, *Porites*, *Pocillopora*, and *Seriatopora*, the polyps

possess only twelve tentacles and twelve mesenteries, but in the great majority of the genera the number of tentacles and mesenteries is very much greater than twelve when the polyps have reached their full size.

The number of septa in a calyx does not always correspond with the number of mesenteries in the polyp that formed it; but, generally speaking, when there are only twelve mesenteries there are only twelve or six septa. In the calices of polyps with a large number of mesenteries there are usually a large number of septa.

It has been suggested, therefore, that, in the first place, the Madreporarian corals with polyps that have twelve mesenteries should be placed in one sub-order, and those with more than twelve mesenteries in another. There are some difficulties, however, in accepting this division of the group at present, as our knowledge of the anatomy of the polyps of so many genera is imperfect, and a rearrangement of our system of classification on imperfect knowledge would be confusing and unsatisfactory. The best plan is to accept the classification that is in general use as regards the families, a classification which is based on the characters of the corallum, and rearrange the order of these families on the lines suggested by our knowledge of the anatomy of the polyps.¹

The arrangement suggested is as follows :

Group A.—Polyps with more than twelve mesenteries.

Family 1. Turbinoliidae.

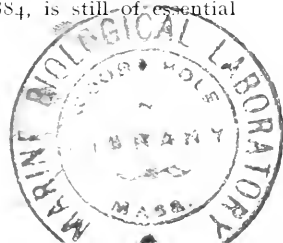
Family 2. Oculinidae.

Family 3. Astracidae.

Family 4. Fungiidae.

Family 5. Eupsammiidae.

¹ For further information on the classification of the Madreporaria the student should consult the beautifully illustrated memoirs by T. Wayland Vaughan, entitled "Recent Madreporaria of the Hawaiian Islands and Laysan," *Smithsonian Institution Bull.* 59, 1907, and "Shoal-water Corals from Murray Island," etc., *Carnegie Publications of Washington*, 1918. In these memoirs reference is given to other papers which are necessary for the identification of specimens. P. Martin Duncan's *A Revision of the Families and Genera of the Madreporaria*, published in 1884, is still of essential importance, and should be referred to.



Group B.—Polyps with twelve mesenteries.

Family 6. Seriatoporidae.

Family 7. Madreporidae.

These families include most of the recent Madreporarian corals, but there are still some recent corals, such as *Pyrophyllia*, *Guynia*, *Bathyactis*, etc., and many fossil corals which cannot, at present, be placed in any of them.

Before proceeding to a systematic description of a few representative genera of each of these families it is necessary to refer briefly to the arrangement of the mesenteries of the Madreporarian polyps and their relation to the septa.

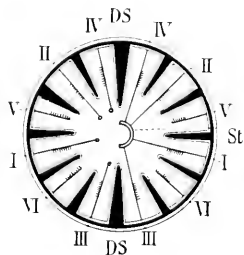


FIG. 6.—Diagram of a transverse section of a Madreporid calyx to show the relation of hard parts (thick lines) and soft parts (thin lines). I-VI, the mesenteries (protocnemes); DS, the directive septa; St, the stomodaeum; III-IV, the directive mesenteries. On the right side of the diagram the section is taken through the stomodaeum; on the left, below it.

It has been found that in the development of the Madreporarian coral polyp there is a stage when there are twelve mesenteries, and that these twelve mesenteries have certain definite characteristics.

The mesenteries are thin laminae of soft fleshy substance passing from the body wall to the stomodaeum or throat. Some of these reach the stomodaeum, others do not.

From each end of the stomodaeum, which is sometimes round and sometimes oval in section, a pair of mesenteries pass to the body wall, called the Directive mesenteries (Fig. 6, III-IV), and in each lateral space between the pairs of directive mesenteries there are four mesenteries, making a total of twelve in all.

These mesenteries are called the Primary mesenteries or Protocnemes, and it may be added they are formed in bilateral pairs, that is to say, at the time of their appearance one member of a pair corresponds with the other member on the opposite side of the stomodaeum. The order of sequence of these mesenteries is indicated by the numbers I-VI in the diagram.

In the families of corals belonging to Group A additional pairs of mesenteries are added to the primaries, but these are unilateral pairs, the two members of a pair being close together on the same side of the stomodaeum. These unilateral pairs of mesenteries are called the Secondary mesenteries or "Metacnemes." In the diagram (Fig. 7) that has been drawn to illustrate this arrangement eighteen unilateral pairs—metacnemes—have been drawn, but it must be noted that in most of the corals belonging to Group A there are more than eighteen metacnemes, and in many cases a very large number. There is one point also which is of particular interest and importance in the arrangement of these mesenteries. The pairs of metacnemes appear in the spaces between the lateral protocnemes, but no metacnemes are ever found in this group in the spaces between the directive mesenteries.

The result of this arrangement is that whereas the lateral protocnemes may be separated from one another in a large polyp by a great number of pairs of metacnemes, the directive mesenteries always stand side by side and can be recognised as the directives throughout life..

But this is not the only character by which the directive mesenteries can be recognised.

One of the functions of the mesenteries is to support the important longitudinal muscles which cause the retraction of the polyps, and the position of these muscles can be seen in a transverse section of a polyp as a series of ridges on one surface only of the mesenteries. In the cases of the directive mesenteries these ridges are on the surfaces opposed to each other, that is to say, they face outwards (see diagram 6, III-IV), whereas in the other mesenteries the muscle ridges face inwards (see diagrams 6 and 7).

This feature of the directive mesenteries is of some importance in the study of the anatomy of the *Astraeid* corals

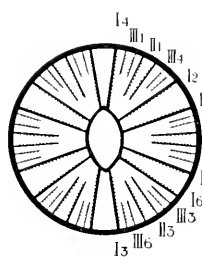


FIG. 7.—Diagram of the mesenteries of the *Astraeid* polyp *Manicina*, showing eighteen pairs of metacnemes. II 1-3, III 1-6. After Duerden.

in particular, because the polyps of some of the corals belonging to this family appear to be entirely devoid of directive mesenteries, and this fact can only be explained by their method of asexual reproduction.

The different kinds of asexual reproduction in the Madreporarian polyps may be arranged in two categories: reproduction by gemmation or budding and reproduction by fission or division into two. Reproduction by gemmation may be intercalicinal when the buds arise from the coenosarc between the calices, epicalicinal when they arise from the

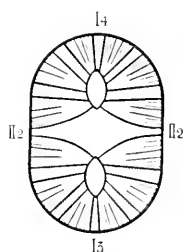


FIG. 8. Diagram to show a stage in the division by fission of the Astraeid polyp *Manicina*. I3 and I4 the directive mesenteries. After Duerden.

outer wall of the calyx, or intracalicular. The buds produced by all these methods of gemmation always show throughout life two pairs of directive mesenteries. In reproduction by fission in the Astraeid corals the mouth and stomodaeum constrict in the middle to form two mouths and two stomodaea (Fig. 8), and when the body wall of the polyp follows suit the metacnemes II 2 take up a position opposite to the directive mesenteries I4 and I5 in the resultant polyps, and thus each of these daughter polyps has only one pair of directive mesenteries. When these daughter polyps are large enough to divide

they each give rise to one with one pair of directive mesenteries and one with none.

And thus it comes about, by a continuation of this process, that in a large colony of Astraeids the directive mesenteries appear to be absent in all the polyps, although theoretically there should be somewhere in the colony two polyps each with one pair.

In the families belonging to Group B, the directive mesenteries and the other protocnemes are formed as in the corals of Group A, but, as they are not succeeded by any series of metacnemes, the normal number of mesenteries in a full-grown polyp is twelve.

In the process of fission in the genera *Madrepora* and *Porites* belonging to this group a new set of twelve mesen-

teries appears in the space between two directive mesenteries. They appear in regular sequence (Fig. 10, A, B, C, D) in bilateral pairs until the full number of twelve is reached. Then the mouth and stomodaeum divide by constriction as in the *Astraeid*, and when the polyp itself constricts two

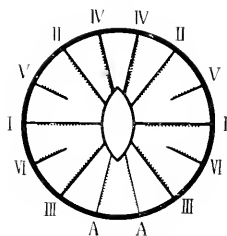


FIG. 9.

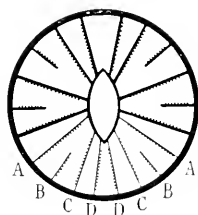


FIG. 10.

FIGS. 9 and 10.—Diagrams of sections of *Porites* to show the new set of Protoconemes is formed in space between the directive mesenteries III, III. In Fig. 9 one pair, A, A, has been added, in Fig. 10 four pairs. After Duerden.

pairs of directive mesenteries are formed for each daughter polyp by the mesenteries marked IV and *f* on one side and III and *a* on the other, that is to say by one old directive mesentery and one new one in each pair (Fig. 11).

Thus it comes about that in these two genera, although asexual reproduction is by fission every polyp in a large colony has two pairs of directive mesenteries.¹

The relation of the hard calcareous septa of the coral cup to the soft fleshy mesenteries of the coral polyp which forms it is a matter of considerable importance for the proper understanding of coral anatomy. The septa are always formed in the spaces between the mesenteries and never in the substance of a mesentery (Fig. 6, p. 32), and, as the septa do not always correspond in number with the mesenteries, the septa of the dried coral afford no trust-

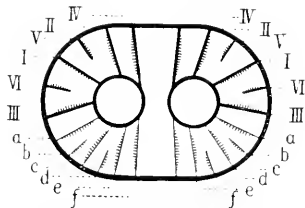


FIG. 11.—Diagram to show a stage in the division of a polyp of *Porites*. Lettering as in Figs. 9 and 10. After Duerden.

¹ J. E. Duerden, "West Indian Madreporarian Polyps," *Mem. Nat. Acad. Sci. Washington*, vol. viii., 1902.

worthy evidence concerning the mesenteries of the living polyp. It may be said, however, that when there are six or twelve septa there are twelve and usually not more than twelve mesenteries, and that when there are more than twelve septa there are always more than twelve mesenteries. In the method of development of the septa there appears to be a remarkable uniformity in corals belonging to widely separated families ; but in view of the fact that our knowledge of coral embryology is still very limited, it would not be right to assume that there are no exceptions to what appears, at present, to be a general rule.

When in the development of the polyp of a solitary coral or the first polyp of a colonial coral the twelve primary mesenteries (protocnemes) have been formed, six septa appear simultaneously in the spaces between the mesenteries. Two of these six septa are always found in the spaces between the directive mesenteries and may be called the directive septa, and the others in alternate intermesenteric spaces. These are followed by another six septa situated in the remaining six intermesenteric spaces.

Twelve septa are thus formed, and, in conformity with the terminology of the mesenteries, these twelve primary septa may be called the "protosepta."

In some cases (*Astroides*, *Balanophyllia*, etc.) the twelve protosepta appear simultaneously, but there are many reasons for believing that the former method of septal sequence is the more primitive.

The formation of the metasepta in the corals of Group A follows very closely the formation of the metacnemes, a single septum appearing in the space enclosed by a unilateral pair of metacnemes. But in some cases septa are also formed in the spaces between the unilateral pairs of mesenteries, and thus a distinction has been drawn between the septa that are formed inside a pair of mesenteries (Entosepta) and those that are formed between these pair (Ectosepta). Further discussion of the very complex problems of septal sequence in recent and fossil corals would require more space than can be assigned to the subject in this book.

With these preliminary remarks on the points of structure

of these corals, which are essential for the understanding of the classification, we may now proceed to the study of the families.

FAMILY I. TURBINOLIIDAE

The corals included in this family are mostly solitary in habit, and are either attached to rocks, shells, and other foreign objects, or in some cases rest freely in or on a sandy sea-bottom.

They may be distinguished from the solitary corals belonging to the other families by being imperforate and by having septa which have usually smooth surfaces ; but if the septa are armed with spines or tubercles, they are not joined together by bars (Synapticula) of coral substance as they are in the Fungiidae.

From the solitary and imperforate corals of the family *Astraeidae*, the *Turbinoliidae* are distinguished by the occurrence in the former of dissepiments or tabulae which shut off the living polyp below from the original base of the calyx, whereas in the latter the spaces between the septa pass right down to the base of the calyx.

The British cup-coral *Caryophyllia smithii* has been described on p. 26. It is found at low tide attached to the rocks near Ilfracombe, on the breakwater at Plymouth, and probably in other localities on the coast of Cornwall and Devon. It is also found at Roscoff on the coast of Brittany and on the coast of Norway. Other species of the genus *Caryophyllia* occur in the Mediterranean Sea, and the genus seems to have a pretty wide distribution in shallow water.

The only other corals belonging to this family that have been found on the British coast belong to the genera *Paracyathus* and *Sphenotrochus*. They occur only in deep water off the Atlantic coasts and may be regarded as among the rarities of our marine fauna.

The genus *Paracyathus*, however, seems to be very abundant in some other localities, and requires a few words of description.

PARACYATHUS.—A large number of specimens of *Para-*

cyathus cavatus were obtained a little while ago attached to the telegraph cable in the Persian Gulf. In form they are not unlike the Caryophyllias, but of a larger size, having diameter of half an inch or more at the margin.

When the coral is carefully studied, however, many features can be noticed in which this coral differs from Caryophyllia. These may be referred to here as an example of the kind of characters that can be used for separating genera and for the identification of specimens.

There is a broad base of attachment as in Caryophyllia which adapts itself to the surface of the support. Outside the cup the costae may be seen extending from the base upwards as delicate ridges. They are not, therefore, covered up by a chalky "Epitheca" at the base as they are in Caryophyllia. The septa are very numerous and covered with minute granulations arranged in a series of longitudinal and radial rows, in contrast to the smooth septa of Caryophyllia. The inner margins of the septa exhibit a number of large nodules which represent the pali, and these pass imperceptibly into the central depressed columella, which is similarly covered with nodules. In Caryophyllia the pali and the columella are quite distinct. Such a technical description is difficult to follow unless the specimens are in the hand, but sufficient has been said, perhaps, to indicate that differences in structure such as these, when found to be constant in a large number of specimens of both corals, are sufficient to justify their separation as distinct genera.

Paracyathus cavatus is also found in the Indian Ocean, and other species of the genus are found in the Mediterranean Sea and elsewhere.

HETEROCYATHUS.—The genus *Heterocyathus* presents us with some features of special interest. It is a small coral about one-third of an inch in height which is found in large numbers at depths of 20-40 fathoms of water off the coast of Natal, in the Persian Gulf, and other localities in the Indian Ocean. An important difference between this coral and those belonging to the family that has been described is, that the free edges of some of the septa meet and fuse, forming triangular chambers in which septa of a lower

order are placed. In other respects it approaches *Paracyathus* in structure, having well-marked costae and a nodular columella. The special point of interest, however, is that the coral always lives in association with a small worm (*Aspidosiphon*) belonging to the Order of the *Gephyrea*, and this is indicated in the dried coral by a small smooth round hole at the side of the base through which in life the worm protrudes.¹

These corals seem to occur always on sandy bottoms, and have no disc of attachment or other means of fixing themselves to rocks, large shells, or other objects of sufficient weight to resist the flow of water.

The association with the worm is an ingenious arrangement to prevent the coral being overturned and smothered in the sand, and to ensure the maintenance of an upright position in which the tentacles of its polyp can catch the floating and drifting organisms on which it feeds, for the *Gephyrean* worm feeds in the sand and thus acts as a kind of muscular root always ready to drag the coral upright again if it loses its balance.

The origin of the association can be seen in very young individuals or by making vertical sections of a full-grown specimen. The young worm begins life by sheltering in a small *Gasteropod* shell (*c.g.* *Cerithium*) like a *Hermit Crab*. The coral larva settles on the outside of the shell by an ordinary base of attachment, and as the coral grows and the base extends it surrounds the shell, leaving only a hole through which the worm can protrude. Growth of the coral does not stop when the shell is completely surrounded, but continues in all directions to form a smooth rounded base perforated on one side by the worm tunnel in the coral substance, which can be traced from the outside to the mouth of the shell. The size and shape of the shell on which the coral larva starts life vary considerably and cause many variations in the subsequent shape of the adult coral. This has led to the splitting of the genus into a large number of quite unnatural species, and subsequently to the amalgamation of these species into one or

¹ As in *Heteropsammia*, Fig. 32, p. 79.

two species which are recognised to be highly variable in form.

More interesting than the settlement of this difficult and highly controversial species question, however, would be the discovery of the determining cause of the association of the worm and the coral. It seems highly probable that if the coral larva settles down on a little shell that has no worm in it, it could not long survive, for it would soon be rolled over and smothered in the sand either by the action of the currents of water or by any fish or crab that passed by.

Does the coral larva, therefore, select shells already inhabited by a worm or does it simply trust to chance? In the latter case, thousands must die for every one that survives. It may be, however, that there is a kind of unconscious selection, the larva finally settling down only on a shell whose stability—due to the presence of the worm—has been tested.

The *Heterocyathus* is not the only coral associated with this or a closely related worm. The same thing is found in the perforate Eupsammiid coral *Heteropsammia*, occurring in the same seas and under similar conditions.

DESMOPHYLLUM.—The largest of the Turbinoliid corals is *Desmophyllum crista-galli*, which attains to a height of 4 or 5 inches and a diameter of $1\frac{1}{2}$ inches at the margin of the calyx. It has been found in deep water in the Atlantic slopes off the British coasts and in other localities. A giant specimen of this species, $5\frac{1}{2}$ inches in height, was found by the *Challenger* expedition in 345 fathoms of water off the coast of Patagonia. The living polyp of this genus has been studied and drawn by de Lacaze-Duthiers.

FLABELLUM.—The widely distributed, and in some localities very abundant, genus *Flabellum* is usually placed in a separate subdivision of the family on account of the peculiar formation of the wall of the calyx.

Most of the specimens belonging to the genus are not round, but oval in section, being, as it would seem, laterally compressed. The longest of the diameters is in the plane of the directive septa. When viewed from the side, *Flabellum* has the shape of a fan with the handle sharply

broken off. The outer wall does not show any trace of costae, but there is a series of more or less well-marked transverse lines of growth. The principal peculiarity of the genus, however, is that the polyp is entirely restricted to the inside of the calyx. It does not overflow, as in many of the corals, so as to cover the whole or the upper part of the outside of the calyx with its soft living flesh. As the outer wall of the calyx is thus wholly exposed to the sea-water, it frequently forms the support of worm-tubes, polyzoa, barnacles, and foreign bodies of various kinds. The process of formation of the wall of the calyx in *Flabellum* appears to be of a different type from that in the other Turbinoliidae, as shown by the absence of costae and the presence of foreign bodies, and it is therefore usually regarded as an epitheca and not as a true theca.

In the younger stages of its life the base comes to a blunt point, terminating in a small disc for attachment to a shell or rock, but when it has attained to a certain size this point is broken off sharply, leaving an oval scar at the base in which the septa are exposed.

After the coral has broken off its base of attachment in this way, one or more pairs of wing-like processes may be formed on the edges of the epitheca, or in some cases hollow root-like tubes grow from the scar.

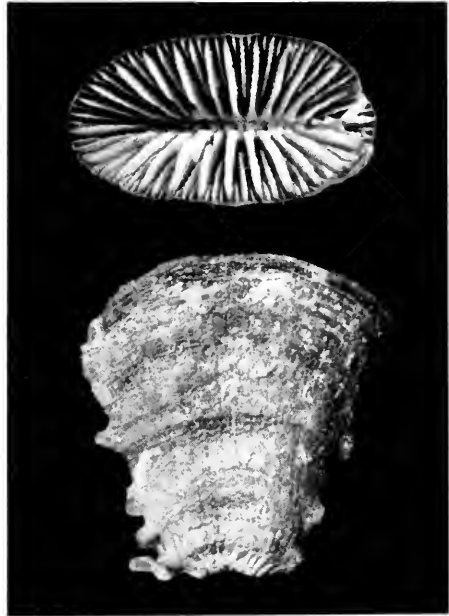


FIG. 12.—*Flabellum rubrum*. The upper figure shows the cavity of the calyx and the septa. The lower figure is a side view showing the lateral processes and the scar at the base. Nat. size.

The latter are clearly for the purpose of attachment to some foreign object, and the former may act as additional supports for the specimens that are imbedded in sand and mud. Specimens taken from the same locality are extremely variable as regards both wings and roots, and it seems probable that these structures are formed in response to the conditions of the immediate environment and cannot be regarded as of any generic or specific importance. A few specimens have been found which were attached to a rock or shell by the side of the epitheca, and such specimens usually exhibit additional abnormalities of form.

FAMILY 2. OCULINIDAE

The corals of this family form large imperforate branching colonies bearing numerous calices, separated from each other by considerable intervals of coenosteum.

As in all the colonial corals, there is immense variety in the size, manner of branching, occurrence of anastomoses, and the distribution of the calices. In recent Oculinidae, however, although the main stem may be nearly an inch in diameter, the branches are usually slender, $\frac{1}{4}$ to $\frac{1}{2}$ inch in diameter, and terminate in blunt extremities. Massive and encrusting forms of colonies are rare.

The genera *Amphihelia* and *Lophohelia* belonging to this family are of special interest, because they are the only large colonial corals that are found in British seas. They are widely distributed in deep water in the North and South Atlantic, in the Mediterranean Sea, in the East and West Indies, and elsewhere. They come within the British fauna off the west coast of Ireland and off the coast of Cornwall.

A general account of the structure of *Lophohelia* has been given on p. 28.

AMPHIHELIA.—The genus *Amphihelia* resembles *Lophohelia* very closely in its mode of growth and ramifications, but is said to differ from it in having a shallower depth of calyx, in a greater regularity of the septa, and in the presence of a true columella. In *Lophohelia*, moreover, there may

exist laminae of calcium carbonate—called the dissepiments—which pass transversely across the inner septal spaces in the depths of the calyx, shutting off the upper spaces where the living polyp tissues are found from the dead coral below; and in some cases true tabulae occur. In this respect the calices of *Lophohelia* approach in structure the calices of the next family of corals—the *Astraeidae*—whereas *Amphihelia*, in retaining the open spaces between the septa right down to the base of the calyx, resembles the *Turbinoliidae* and the other genera of the *Oculinidae*.

There is, however, so much variation in all these characters in both genera, that it is sometimes difficult to determine without most careful examination whether a given specimen is an *Amphihelia* or a *Lophohelia*. This difficulty is increased by the frequent occurrence in specimens obtained from some localities of the natural grafting of the two genera. Specimens are found of which one branch may be a true *Lophohelia* and the others *Amphihelia*, and when the place where the branches join is carefully examined, even in sections, no boundary line can be distinguished to indicate where the *Lophohelia* tissue begins and where the *Amphihelia* tissue ends (Fig. 13). Such grafts might readily lead to a hasty but probably erroneous conclusion that the two forms are not distinct, but are only environmental variations of the same genus and species.

It is not known how this grafting takes place, but as de Lacaze-Duthiers¹ remarks: "La puissance blastogénétique est des plus actives dans cette espèce (*i.e.* *Amphihelia oculata*). Tout ce qui touche à une partie du zoanthodème vivant est fixé, retenu et recouvert par le sarcosome d'abord, et plus tard par le tissu scléreux." Worms, molluscs, bryozoa, and other living things are caught, enveloped by the soft coenosarc, and subsequently covered by the hard coenosteum, and it seems probable, therefore, that when a *Lophohelia* larva settles on a branch of *Amphihelia*, or *vice versa*, and begins to grow, the base of the young colony becomes, in like manner, entirely submerged in the growing

¹ H. de Lacaze-Duthiers, "Zoanthaires sclérodermes," *Arch. Zool. Expér.*, 3^o, v., 1897, p. 143.

coenosteum of the host, and is thus given a firm attachment



FIG. 13.—In the lower part of the figure is seen a branch of *Lophohelia* showing two calices on opposite sides. In the upper part of the figure the *Lophohelia* is seen in blastogenic fusion with an *Amphihelia* with much smaller calices. Nat. size.

for the subsequent growth of the colony. The remarkable

feature of the case is that, owing to the similarity in minute structure of the coenosteum of the two genera, all trace of the line of fusion is lost.

In both these genera anastomoses of the branches, formed in the same manner by the grafting of one colony on another or of one branch with another, frequently occur, giving rise to great tangled masses of coral branches, with various kinds of worm-tubes and shells deeply imbedded in them (Fig. 5, p. 28).

To write an accurate description of such a mass would require a great deal of time and patience, as it might consist of three or four species, each showing a great range of variation in the size of the calices and the characters of the septa and columella, all of which would have to be carefully studied before an approximate estimation of the number of individual corals that have taken part in the composition of the masses could be made.

The only account of the living polyps of these two genera that we possess is that of de Lacaze-Duthiers. In both genera the living tissues are very transparent, but show a pale yellow colour, which is more pronounced round the mouth and on the oral disc. The tentacles correspond in number with the septa, and vary in size according to the order of the septa above which they are situated, the tentacles above the primary septa being larger than those above the secondary septa, and those above the secondary septa larger than those above the tertiary septa. They have a pale yellow colour and are speckled with white spots representing nematocysts or groups of nematocysts, and at the extremity, which is pointed, these spots are so numerous and closely grouped together that the tentacle seems to have a bright white tip. Minor differences between the genera observed by de Lacaze-Duthiers are, that in *Lophohelia* the tentacles are relatively shorter and thicker than in *Amphihelia*, and that the size of the tentacles in the former is more irregular as regards the order of the septa than it is in the latter. Fowler has also pointed out that in *Lophohelia* there are no directive mesenteries, but that in the *Amphihelia* they are present.

OCULINA.—The genus *Oculina* belonging to this family is found in a few fathoms of water in the warmer tropical seas. Like the other genera that have been described, the corallum is sparsely branched, and sometimes shows anastomoses and fusions of the branches.



FIG. 14.—*Oculina*. A small piece of a branch of a large colony. Nat. size.

The coenosteum is very hard and solid. The calices are relatively more numerous and very shallow, and are usually arranged in steep spiral rows on the branches. The rims of the calices project a little from the surface, giving it a warty or verrucose appearance. The number of septa varies, but is usually about twenty-four, and standing opposite the free edges of the principal orders of the septa there are pali. The columella is variable, but frequently consists of a few short pillars very similar in appearance to the pali.

FAMILY 3. ASTRAEIDAE

The family of the *Astraeidae* or Star-corals is, in respect of variety of structure and number of generic forms, the largest and most difficult of all the families of the *Madreporaria*.

The family played an important part in building up the coral reefs of the Jurassic, Cretaceous, and early Tertiary times, but in later Tertiary and in recent times, although still very abundant in some localities, they take a second place in reef-building powers to the more vigorous and

rapidly growing genera of the younger families—the Madreporidae and Poritidae—of the Perforate corals.

Most of the Astracidae are colonial corals, and give rise by fission or gemmation to large heavy rocks of limestone, usually spherical or lobed in form, and rarely, among recent genera, dendritic in growth, and, if dendritic, never dividing up into pointed terminal branches.

The calices are usually set close together, and in many genera are actually in contact with one another, so that there is little or no coenosteum between them. The septa are numerous, and may be entire and smooth as in the "*Astræes inermes*" of Milne-Edwards and Haime, or dentate, spined, or ragged as in the "*Astræes armés*" of the same authors. But the septa never meet and fuse together as they approach the centre of the calyx as in some of the Eupsammiidae (see p. 75), nor are they connected together by synapticula as in the Fungiidae.

One of the most important features of the family is that as the calyx increases in length by upward growth at the surface, the lower part of the cavity of the calyx becomes shut off from the upper by calcareous structures, for which we may use the general term "*Endotheca*." The polyps and other tissues of the coral are entirely confined to the surface and to the cavities of the calices down to the level of the endotheca. It is the presence of endotheca which is the only character to distinguish some genera of Astracidae from genera of Oculinidae and of Turbinoliidae, which in other respects are very similar to them.

There is unfortunately some confusion in the use of the technical terms that are employed for the different kinds of endotheca, and it is difficult to give any terms a very precise definition owing to the great variety of form that the endotheca assumes, but the diagrams in Fig. 15 will show the three principal varieties that are found.

When the endotheca is in the form of transverse plates, the plates are called *TABULAE*; when it is in the form of irregular laminae, the laminae are called *DISSEPIMENTS*; when it is more or less of granular consistency, filling up the

spaces and sometimes fusing into solid bars and plates, the substance is called STEREOPLASM.

GALAXEA.—The genus *Galaxea*, widespread on East Indian tropical reefs, is a genus which can be easily identified (Fig. 16). The general form is very variable, as in all the genera of the *Astracidae*, but the colony is frequently dome-shaped or hemispherical, sometimes throwing out thick lobes or branches, but never being completely dendritic.

The calices stand up from the free surface of the coenosteum as vertical cylindrical columns 5-10 mm. in height. Each calyx is about 5 mm. in diameter, and separated from its neighbours by a distance of about the same measurement.

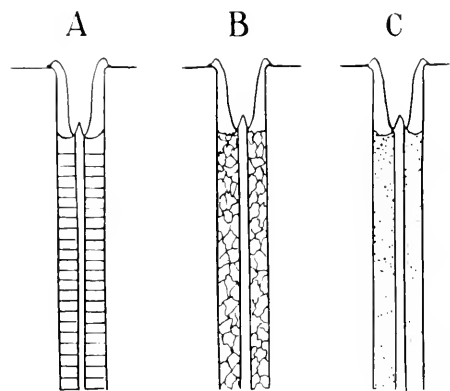


FIG. 15.—Diagrams to illustrate the three principal kinds of endotheca. A, tabulae; B, dissepiments; C, stereoplasms.

There are twenty-four conspicuous septa, twelve large and twelve small, alternating with one another, and in some calices there may be seen, in addition, twenty-four minute septa between the more conspicuous ones. The septa are exsert, that is to say they project upwards, above the lip of the calyx wall. There is no true columella, but the larger septa are connected at the base of the cup by dissepimental bars or trabeculae. There are no pali. The surface of the septa is rough, but is not armed with spines.

The common coenosteum lying between the bases of the calices, which in this case is called the "Peritheca," is marked by a number of small blister-like swellings, and is therefore technically called "Vesiculate."

In certain parts of the colony where growth is active, such as the free edges or the ends of the lobes, a number of small calices can be seen. These small calices have been

formed by the young polyps which have arisen as buds from the peritheca. This is a very important point to grasp if the very difficult and perplexing problems of the classification of the Star-corals are to be understood. For in every modern system of classification great stress is

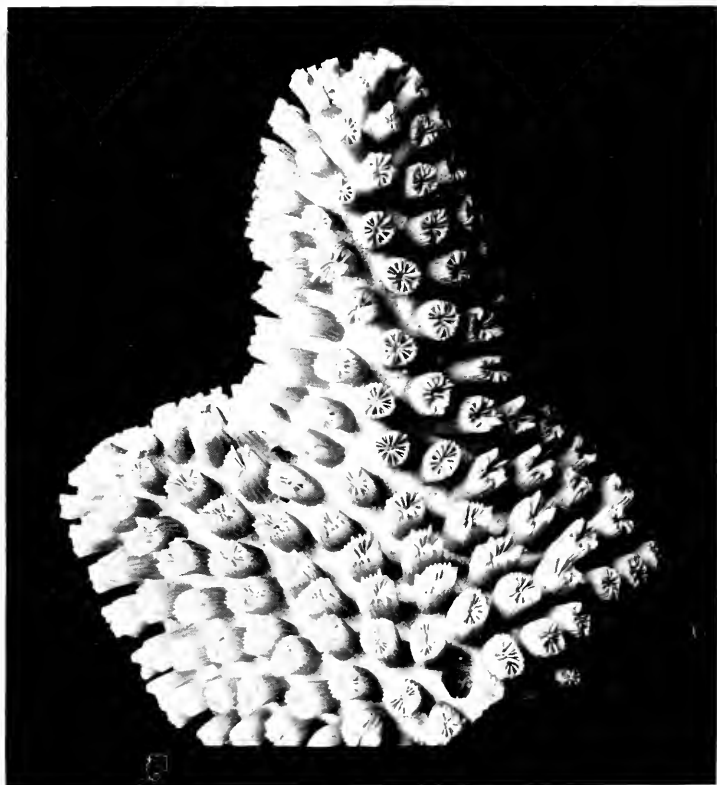


FIG. 16.—*Galaxea caespitosa*, Malay Archipelago. Nat. size.

laid on the method of asexual reproduction found in the colonies.

In *Galaxea* and many others this method of reproduction is by budding or gemmation, and by that particular kind of gemmation which is known as perithecal or intercalicinal gemmation. The particular method of gemmation is not

always constant, and, in some forms of *Galaxea* even, some of the buds may arise from the outer wall of the calyx, a form of gemmation that is called "Epicalicinal" or "Épithecal."

When the *Galaxea* colony is alive, the soft flesh covers the whole surface of the colony as with a mantle. It is not locked into the corallum, as it is in the Perforate corals, by a system of canals perforating the subjacent hard parts. When the colony is killed, therefore, parts of the tissues as they become hardened are often detached, or may be detached with a little manipulation with needles, showing that this flesh is entirely superficial.

The polyps show a crown of twenty-four simple tentacles surrounding a centrally placed mouth, and there are twenty-four mesenteries, of which two pairs are directive mesenteries, in the fully developed condition.

The colour of the living polyps probably varies in different localities, but in a specimen observed by the author on the reefs of Celebes they were of a bright emerald green colour, the expanded colony, as seen through the clear water in the sunshine, being one of the most brilliant of the many beautiful corals of the locality.

FAVIA.—The second type which may be taken to illustrate the structure of the *Astraeid* corals is a genus which is, perhaps, most correctly called *Favia* (Fig. 17). But in this case, as in many others of the same family, the student will find great difficulty in coming to a definite conclusion as to the correct generic name of a specimen owing to the differences of opinion expressed by those whose detailed study of Madreporarian structure has given them the right to be regarded as authorities on the subject. Apart from questions of the law of priority in nomenclature, there is the difficulty in this group arising from the fact that there is so much variation in the species, and there are so many closely related genera that many perplexing examples occur of intermediate or overlapping species and genera. The consequence is that the old genera have been split into several new genera and the new genera reunited under the old generic name in a way that has made it very difficult to maintain an accepted or acceptable nomenclature.

Oken's genus *Favia* was established in 1815 for a section of the older genus *Astrea* of Lamarck, and it includes species of corals that have been described under the generic names *Orbicella*, *Heliastrea*, *Plesiastrea*, etc., etc.

The corals of this genus are usually hemispherical or almost spherical in shape, without lobes or branches but

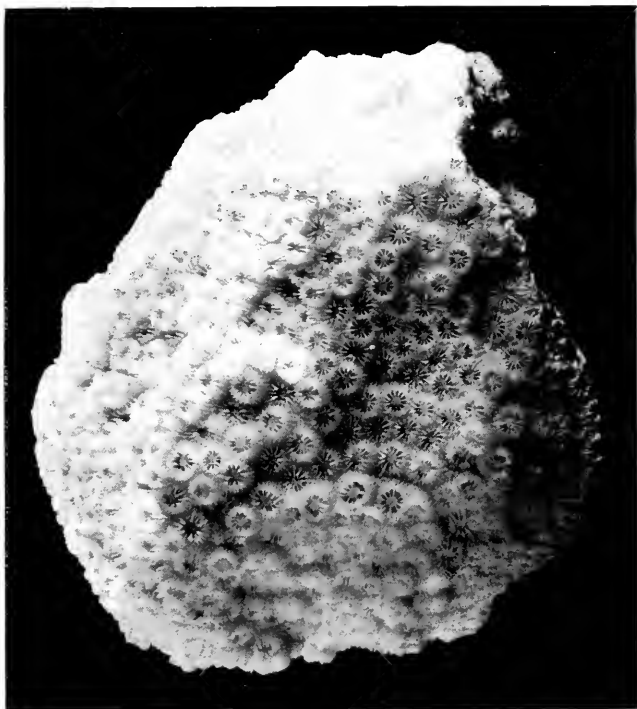


FIG. 17.—*Favia*. A small specimen. Nat. size.

sometimes encrusting in habit. The surface of the coral consists of a large number of close-set calices about 10 mm. in diameter which project but slightly above the general level of the scanty peritheca between them. The calices are usually circular in outline, but in many specimens where they seem to be more crowded together than in others they become angular and distorted, but never regularly hexagonal.

The septa vary greatly in number, but in a typical calyx

there are about twelve large septa alternating with twelve smaller septa. The larger septa are usually slightly exsert, and are continued over the lip of the theca into twelve costae, which are extended on to the peritheca to meet the costae of neighbouring calices.

In most examples there is a trabecular columella to which the larger septa are joined, but this structure is rudimentary in others.

If a large colony be carefully examined some calices will be found more elongated than the rest and show a constriction which indicates a division of the calices into two equal or unequal portions. This may be taken as a sign that the usual method of increase in the number of polyps is by the process of splitting into two or by fission.

The process of fission is brought about in these corals by the increase in one diameter of the calyx accompanied by an increase in the number of septa, and this is followed by a constriction of the calyx wall in a plane at right angles to the diameter which has increased in length and the constriction is continued until the single calyx is divided into two calices. The fission of the coral polyp is on the same plan as that of the calyx, an increase in the number of the mesenteries being followed by a vertical plane of constriction of the body wall of the oral disc and of the crown of tentacles; and finally, the division of the polyp vertically into two polyps.

This method of asexual reproduction of the individuals of a colony of *Favia* is undoubtedly the most common, but it is not the only one, because at the base or, in the encrusting forms, at the growing outside edge of some specimens small calices may be found arising from the coenosteum between the other calices. Increase in numbers of individuals, therefore, may occur not only by fission but also by gemmation in this genus.

In the anatomy of the polyps of *Favia* there is one point of special interest to which attention should be drawn. In the polyp of *Galaxea*, as already mentioned, there are two pairs of directive mesenteries as in most of the sea-

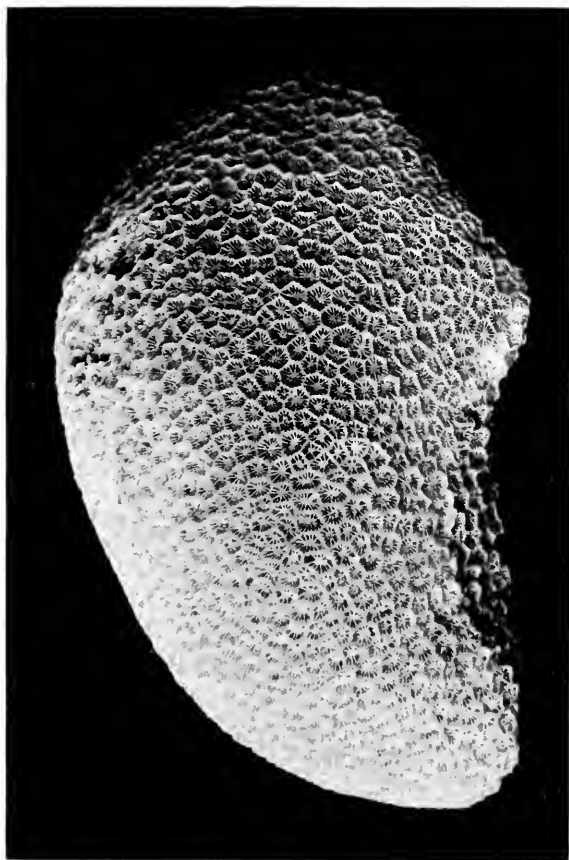


FIG. 18.—*Goniastrea*, $\frac{2}{3}$ nat. size.

anemones and Madreporarian coral polyps, but in the Astreaeid coral polyps that divide by fission the directive mesenteries are usually absent. Duerden, who first called attention to this fact, considered that the absence of directive mesenteries in the polyps of an Astreaeid colony could be taken as a sign that the method of reproduction was by fission, and *vice versa* that the presence of the directive mesenteries was a sign that the method of reproduction was essentially one of gemmation. There are some exceptions, apparently, to this interesting and important generalisation, for in the genera *Cladocora*, *Stephanocoenia*, and *Solenastrea*, which are apparently fissiparous, the directive mesenteries occur, and in two species of *Favia* investigated by Matthai the polyps that arise by gemmation do not possess directive mesenteries.

GONIASTRAEA.—In the genus *Goniastrea* (Fig. 18), another widely distributed coral on the tropical reefs, the calices are so crowded together that the thecal walls are actually in contact, the common coenosteum being apparently absent. As a result of this crowding the calices have lost their round contour and become angular, but they do not form a hexagonal pattern, some being triangular, some roughly quadrangular, and others pentagonal or irregular.

Among the more irregular forms a few calices may usually be found with a constriction in the middle which shows that the usual method of reproduction is by fission.

In the characters of the septa and in some other respects the genus *Goniastrea* is very similar to *Favia*.

We have seen that in *Favia* and *Goniastrea* some of the calices become elongated and then constrict to form two calices. In other genera the elongation takes place, but the constriction is delayed so that the calices assume the form of long straight or sinuous grooves, provided on each side with rows of septa and separated by ridges from similar grooves representing the neighbouring calices. The extreme forms of this modification are seen in the group of Astreaeids commonly known as the Brain corals, from the fact that these sinuous calices give the rounded surface of

the coral an appearance similar to the convoluted surface of the human brain.

Between the Brain corals and the *Favia* type of coral, however, there are many intermediate forms which in a series show an increasing number of elongated sinuous calices among the round or angular ones.

DICHOCOENIA.—An example of such an intermediate stage is shown in the figure of a specimen of the genus *Dichocoenia* (Fig. 19). In this genus some of the calices seem to be circular in outline, and, as they are in some

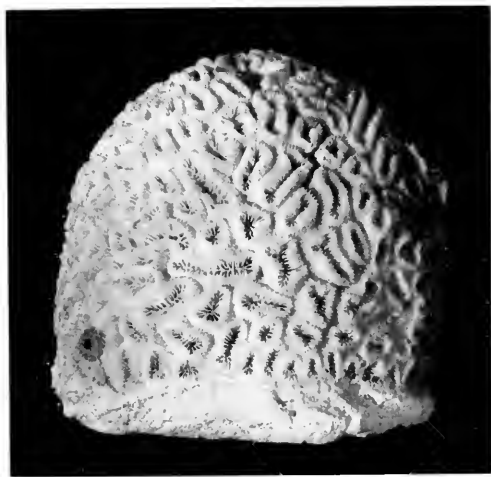


FIG. 19.—*Dichocoenia pulcherrima*. A small specimen. Nat. size.

species separated by a scanty vesicular coenosteum, have an appearance somewhat like that of *Favia*, though amongst them there are many elongated straight or sinuous calices which show no trace of constriction. But these elongated calices are relatively short as compared with the long labyrinthine calices of a true Brain coral.

The septa of *Dichocoenia* are well developed, slightly exsert, and, as in *Favia*, are continued over the lip of the calyx wall as costae which meet the costae of neighbouring calices on the peritheca.

The most familiar of the Brain corals are those included

in the genera *Meandrina*, *Coeloria*, and the closely related genus *Leptoria*.

MEANDRINA.—In *Meandrina* the calices are principally represented by long sinuous valleys, but in places more circumscribed calices may be found. Between the valleys there are ridges representing the fused walls of the calices, for in these genera there is no peritheca as there is in *Dichocoenia*. There are numerous close-set septa and a median spongy columella. The general appearance of the surface of one of these Brain corals, as they are seen in a museum, with all the soft fleshy parts removed, is that of a labyrinth or maze of valleys without any regularity or order in their arrangement; and, if a single valley is traced for any distance and found to divide into two valleys or to run into another valley, it is difficult to believe that they are essentially the same thing as, or, to use the scientific phrase, morphologically homologous with, the calcareous cups that support the well-defined polyps of such a coral as *Galaxea*.

The series of intermediate forms which have been described suggests that it must be so; but the evidence would not be complete without some knowledge of the characters of the animals that construct them.

In a living Brain coral the valleys are covered by a continuous lamina of soft fleshy substance rising a few millimetres above the hard coral substance, and this lamina is perforated at intervals of 2 or 3 mm. by a number of slit-like holes, the polyp mouths. The lamina rises on each side to the ridge which is provided on both sides with two rows of short stumpy tentacles.

The colour of the living expanded polyps of the Brain corals is often very vivid and brilliant. The oral lamina is bright green with the mouths outlined in brown. The tentacles are sienna-brown, becoming paler as they are extended in full expansion in search of food. When the polyps are contracted, however, the green colour is lost owing to the tentacles folding over the lamina, and the whole coral seems to be covered by a darkish brown slime. There is a great deal of variation in the shades and tones of colour in these as in other corals; and it is interesting that the notes

the author made of the colour of a Brain coral in North Celebes are almost identical with the descriptions of the colours of *Meandrina labyrinthica* by Duerden in Jamaica.

But to return to the anatomy of the polyps. Each of the mouths that are found in the lamina leads into a short throat (stomodaeum) which is suspended in the general cavity by an attendant set of mesenteries. There is free

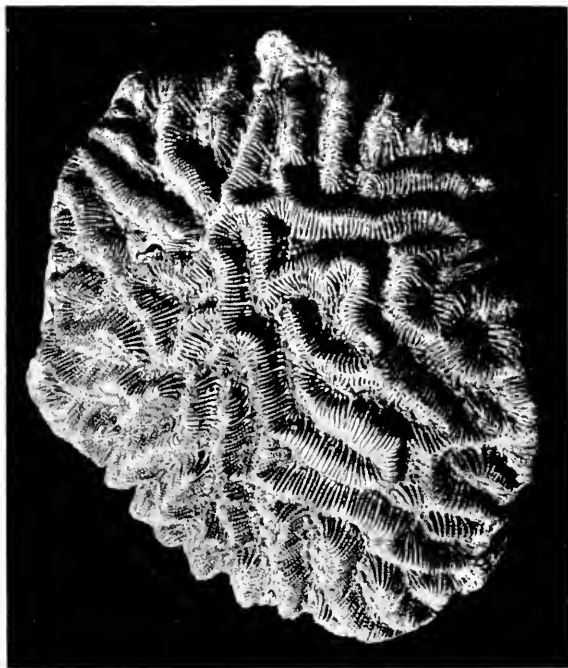


FIG. 20.—*Meandrina*. Nat. size.

communication between any one mouth and the cavity, between the individual mesenteries of a set and the cavity of the sets of mesenteries on each side of it. If, therefore, we try to maintain that each mouth with its stomodaeum and its set of mesenteries corresponds with a polyp, an individual polyp, of such a coral as *Galaxea* or *Favia*, we are met with the difficulty of determining, in the absence of a limiting body wall, where one polyp ends and the others

begin, and also what number of tentacles of the ridges legitimately belong to one polyp and what to the next. It is difficult to think of an individual which has no well-defined limits. But the difficulties are no less if we try to maintain that a whole valley with its ridges corresponds with the single polyp of a *Galaxea*. It is quite conceivable that an individual may have two or indeed any number of mouths, or two or a reasonable number of sets of organs. But if we study the anatomy of *Meandrina* carefully we find that one valley communicates with the others as freely as one set of organs communicates with another in a single valley, and therefore our new proposition leads to the conclusion that the whole set of mouth and organs represents only one individual polyp. Which, it might be said, is absurd. There is no solution to this problem unless there is a perfectly clear conception in the mind of the writer or reader of the meaning of the word "individual." The only reasonable solution of the difficulty is, as suggested in Chapter I., to abandon the use of the term Individual as applied to Polyps in organic continuity and to regard the coral as a whole as the only true "Individual."

EUPHYLLIA.—Another group of *Astraeid* corals is represented in most large collections by the genera *Eusmilia*, *Euphyllia* (Fig. 21), and *Mussa*. From a thick stem attached to a rock or to another coral the colony divides irregularly into two or three stout branches, which may again subdivide. Each terminal branch ends in a relatively large calyx, in a typical form 20-30 mm. in diameter. The calices may be round or oval or triangular, or more irregular in outline, and they may show the constrictions which are evidence of division by fission. The method of colony formation is technically known as "caespitose," as it has a slight resemblance to the method of branching of some turf plants.

The septa are numerous and very variable in number, according to the size of the calyx. There seem to be three or more orders of septa. The septa of the first order are large and almost reach the centre of the calyx, those of the second order alternating with those of the first are smaller,

while those of the third and subsequent orders are very small, and only to be found in the upper part of the calyx.

The differences between the three genera are not of very great importance, and it may be that when some one has the courage to revise the system on which the genera of these corals is based they will be amalgamated. In *Eusmilia*,



FIG. 21.—*Euphyllia*, East Indies. $\frac{3}{4}$ nat. size. The line called the "Edge-zone" can be distinctly seen about $\frac{1}{4}$ inch below the rim of each calyx.

according to the system in vogue, there is a spongy columella at the bottom of a deep fossa, in *Mussa* it is rudimentary, and in *Euphyllia* it is absent. *Mussa* differs from the other two in having widely separated spines on the theca and dentate septa, and also in having the septa very much more exsert. Apart from the difference as regards the columella, a very variable character on which to base a generic distinction, *Eusmilia* and *Euphyllia* are almost identical. It has been the custom, however, to refer specimens from the

West Indies to the genus *Eusmilia* and specimens from the East Indies and Pacific to the genus *Euphyllia*.

The characters of the polyps in the three genera seem to be very much alike. In a living specimen there is an oral disc surrounding the mouth, and at the margin of the calyx there is a large number of short finger-shaped tentacles. Outside the margin of the calyx the soft living substance extends downwards for a few millimetres like a finger-stall covering the hard corallum. This outer skin is called the Edge-zone by English authors (in German "Randplatte"). Below the Edge-zone the corallum is exposed, and is usually subject to the attacks of boring worms and other destructive agents, or is partly protected by *Polytrema* or *Polyzoa* or other encrusting forms of animal and vegetable life.

The "Edge-zone" has another point of interest, as its lower limit can be fixed in the coral after the removal of the soft parts by the texture of the surface. Above the limit the surface is compact and marked by more or less well-pronounced costal ridges; below the limit the surface is chalky in texture, and there is no trace of costal ridges.

According to Bourne, "the *Mussa* of Diego Garcia is of a dull brown colour, with olive-green disc and tentacles." According to Ehrenberg, the polyps are pale brown with a golden-yellow disc. Duerden describes the colours of another genus—*Isophyllia*, closely related to *Mussa*—found on the reefs of Jamaica as follows: "The prevailing colours are dark green, brown, and yellow, with minute, opaque white, superficial granules distributed practically all over. The yellow colour predominates along the thecal ridges and the green along the valleys. Irregular, opaque white, cream, or green patches are sometimes present on the disk, ending in streaks towards the periphery, that is, in the region covered by the overfolding column wall."

The *Astraeidae* that have so far been described have the more characteristic massive, spherical, or lobed form of the members of this family. Some statement must now be made concerning the corals that clearly belong to the family but have a different appearance. They may be arranged in

three categories, (1) the foliaceous *Astraeids*, (2) the dendritic *Astraeids*, and (3) the solitary *Astraeids*.

MERULINA.—This coral (Fig. 22), found in the Indo-Pacific Oceans, is one of the commonest of the foliaceous *Astraeids*. Its general form is that of a huge cabbage-like vegetable, attached by a thick stem, and sending off, more or less horizontally, a few large leaves or fronds.

When the upper surface of one of these fronds is examined



FIG. 22.—*Merulina*. The upper surface of a part of a frond. Nat. size.

it has the appearance of a raised map of a mountainous country, a complex of hills and valleys with a general inclination from the base to the periphery of the frond (Fig. 22). Here and there on the surface of the fronds there are irregular raised patches, which would correspond with high mountain peaks. When the slopes of the valleys are examined more carefully with a magnifying glass, they are found to be traversed by a series of parallel laminae, which can be recognised as the septa of an *Astraeid* coral. In some places

there may be found little round pits or oval depressions, where the septa have a tendency to radiate as from a common centre, but there are no other indications of anything corresponding with discrete calices.

We have, in fact, in *Merulina* as in the Brain corals, a complete continuity of the calyx units that are so well defined in the more primitive compound *Astraeids*.

The general form and surface markings of *Merulina* might

possibly lead to a confusion with another coral belonging to a different family, namely, *Pachyseris* (Fig. 29, p. 75).

It is therefore important to note that the surfaces of the septa are armed with a profusion of spines, but that these spines never meet across the interseptal spaces to form bars (synapticula), binding the septa together as they do in the family to which *Pachyseris* belongs.

ECHINOPORA.—Another foliaceous *Astracidae*, not infrequently found on the Indian and Pacific coral reefs, is *Echinopora*. The thin lobes or laminae of this coral exhibit a very different arrangement of the calices, as they are far more clearly defined and separated from each other by considerable intervals of coenosteum. In the centre of each calyx there is a broad and conspicuous spongy columella, and from this radiate a number of thick septa, continuous over the lip of the calices with very well-marked costae, spreading over the coenosteum and joining up with the costae of neighbouring calices to form continuous ridges. As the generic name implies, *Echinopora* is also characterised by the rich endowment it possesses of sharp spines. The septa are edged with rows of strong sharp teeth, which are particularly well developed in the neighbourhood of the columella, and the whole surface of the coenosteum is armed with numerous spines.

CLADOCORA.—Of the recent dendritic *Astracidae*s, the most familiar is *Cladocora*. One species (*C. arbuscula*) of this genus is found in the Mediterranean Sea, but it is more characteristic of the warmer waters of the Atlantic Ocean.

“ Small bush-like colonies of this species occur in numbers in the shallow waters of Kingston Harbour in Jamaica and at other points around the coast, either free or attached to loose pebbles or shells. Larger colonies are found in water of from three to six feet, and thickly incrust the bottoms of boats plying in the harbours ” (Duerden).¹ The branches of this dendritic coral terminate in small columnar calices 4.5 mm. in diameter.

Each calyx has a variable number of exsert septa, several pali, a well-developed columella, and simple granular

¹ *Mem. Nat. Acad. Sci. Washington*, vol. viii., 1902, p. 558.

or spiny costae. The most usual method of asexual reproduction is by lateral columnar gemmation, but a process, called fissiparous gemmation by Duerden, also, but rarely, occurs.

The expanded polyps are light brown in colour, and are provided with twenty-four to thirty-six slightly knobbed tentacles arranged in three or four cycles. The margin of the disc has sometimes a bright iridescent colour. As with nearly all the gemmiparous *Astraeids*, the polyps of *Cladocora* are provided with two pairs of directive mesenteries.

The genera of *Astraeidae* that do not form colonies (*Astraeidae simplices*) are among the rarities of museum collections, and our knowledge of their anatomy is very imperfect.

The essential difference between a simple *Turbinoliid* coral and a simple *Astraeid* is that in the latter the base of the cup is more or less blocked by endotheca.

But some of them differ from the ordinary *Turbinoliids*, and resemble some of the *Astraeids* in having the septa armed with numerous spines. Any differences which may exist in the structure of the polyps have yet to be discovered, and it may possibly be proved that the separation of the two groups is unnatural. The solitary *Astraeids* do not seem to be abundant anywhere in modern times; a solitary specimen here or a half-dozen specimens there is the only booty of the fortunate collector. In no locality, so far discovered, are they found in great numbers. They are not confined to any one region, but may be found in deep or in shallow water in the warmer seas of the world.

FAMILY 4. FUNGIIDAE

The characteristic feature of this family is that the septa are united by synaptacula. The synaptacula are bars of solid coral substance that pass horizontally from one septum to another and in doing so perforate the mesenteries. In some respects the *Fungiidae* are intermediate between the imperforate corals previously described and the perforate corals, for, although the septa and the theca are usually

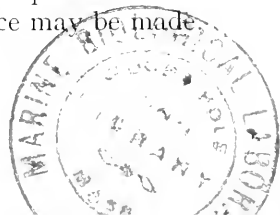
imperforate, there are some forms in which either septa or theca or both are porous. It is quite clear that any attempt to divide this family into two groups on the character of the perforation or imperforation of the corallum would be unnatural and unsound.

The genus *Fungia* (Fig. 23) is a solitary coral and can readily be distinguished from the solitary corals of other families of Madreporaria, but nearly all the other genera are compound or colonial corals, the corallum being built up by the activities of a large number of polyps, and many of these seem to approach very closely in structure to corals belonging to other families. It is in such cases that the determination of the presence or absence of synaptacula becomes a matter of great importance.

According to the system adopted by Duncan and subsequent authors, the group of corals which is here called Fungiidae constitutes a separate section of the Madreporaria called the Madreporaria fungida, and this section is divided into a number of families. Of these families the one called Fungiidae includes the genera *Fungia*, *Halomitra*, *Herpetolitha*, etc., the family Plesiofungiidae includes the important genus *Siderastraea*, and the Lophoseridae includes the genera *Agaricia*, *Pachyseris*, *Pavona*, etc. The Plesiofungiidae are in some respects a transition group between the Fungiidae and the *Astraeidae*, and an extinct family, Plesioporitidae, forms a transition group between the Fungiidae and the Madreporidae.

FUNGIA.—The best known and most widely distributed of the genera of the Fungiidae is the "Mushroom coral," *Fungia*. On many of the tropical coral reefs of the old world it can be collected in cart-loads, and attracts attention not only on account of its size—for it may be a foot in diameter—but on account of its curious resemblance to the inverted disc of a mushroom. Moreover, it differs from the other corals of the reef in being free, in the adult condition, so that it can be lifted and examined without forcibly detaching it from any basal support.

The history of our knowledge of *Fungia* presents some features of special interest to which reference may be made.



The early belief that the Fungia was simply a mushroom which had, in some mysterious way, fallen into the sea and been turned into stone was finally disposed of by Rumphius in 1684, who proved conclusively that the structure of Fungia is totally different from that of a Fungus.

But Rumphius did more than that, for he gave, for the first time, an account of the coral polyp. He said that when the coral is seen alive in the water it is covered with an animal-like ("diergelyke") mucus, that it is provided with innumerable oval tentacles ("langwerpige blaasjes"), and that when it is taken out of the water this mucus and the tentacles contract between the septa. Although he compared the mucous substance of the Fungia with that of a jelly-fish ("zeequalle"), he was not sufficiently in advance of his time to declare boldly that it was an animal and thereby anticipate the discovery by Peyssonel and Ellis, a century later, of the animal nature of corals, but was contented with the somewhat vague conception that it is intermediate between a stone and a zoophyte.

One of the most interesting facts that have been discovered about Fungia is that the familiar large unattached specimens are preceded in development by a stage in which they are attached by a short stalk to a rock.

The first reasonably clear and illustrated account of this stage was given by Stutchbury in 1830, but it was not until quite recent times that a complete description of the way in which the Fungia is formed from the attached stalk and is subsequently detached from it has been given by Bourne.¹ It is interesting, however, to find that the stalked form did not escape the notice of Rumphius,² who says that "sometimes a little foot can be seen on the underside by which it is attached, but not firmly, to the rocks."

In a large collection of specimens of Fungia there can usually be found at least one which is almost completely circular in outline, and it is convenient to use such a form for a first study of the structure of the genus. Variations of this type can be studied later.

¹ G. C. Bourne, *Trans. Roy. Dublin Soc.* v., 1893.

² Rumphius, *Amboinsch Kruidboek*, vol. vi. Book xii. p. 247.

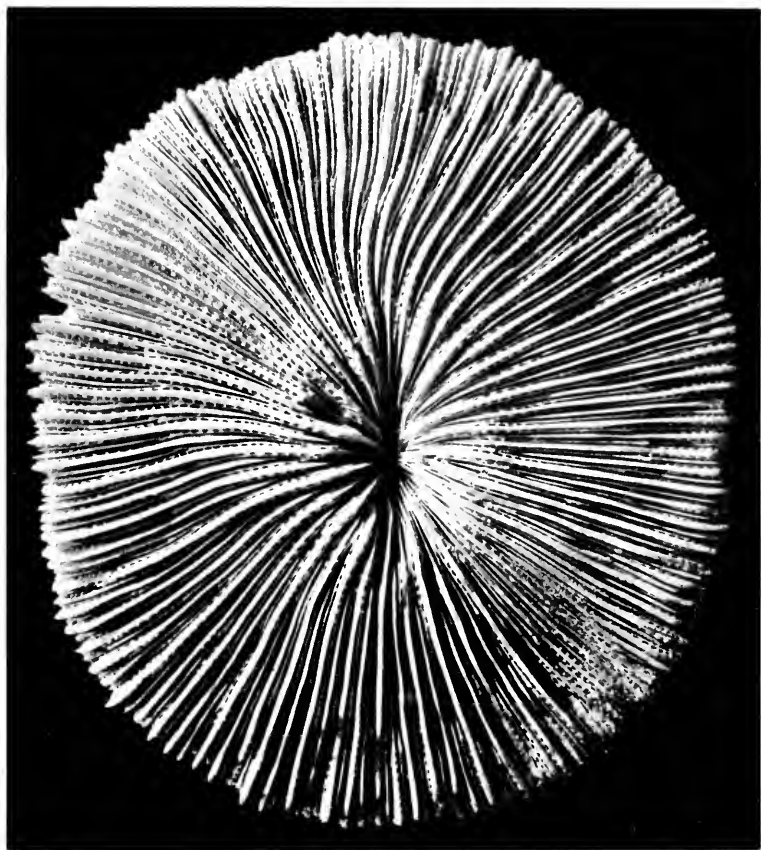


FIG. 23.—*Fungia*. The septa in some places in this specimen are rather water-worn, exposing the synapticula more clearly than in perfect specimens. Nat. size.

The upper surface of a *Fungia* of this type is slightly convex and frequently raised into a shallow mound towards the centre. The under surface is slightly concave, so that the coral rests on its margin when placed on a flat table. The upper surface is provided with a very large number of vertical radially disposed laminae—the septa—with sharp dentate or sinuous edges. The under surface is marked by a corresponding series of shallow radial ridges—the costae—armed with rows of blunt tubercles. Between the ridges on the under side there is solid coral substance representing the theca of the cup corals. In the centre of the under surface there may be an ill-defined circular area, better recognised in small than in large specimens, somewhat raised or depressed and free from costal ridges. This will be referred to as the “scar.”

In the centre of the upper surface there is a deep groove or fossa from which the septa radiate to the margin of the coral. This fossa may be taken as an indication that the coral does not exhibit perfect radial symmetry but may be divided into two laterally symmetrical halves along a diameter, which may be called the directive diameter and is parallel with the median line of the fossa.

The septa are so numerous and close set that there is difficulty in counting them and reducing them to a system ; but in a good specimen a large septum can be seen passing from each end of the fossa to the periphery in the same plane as the directive diameter. These are the directive septa. And on each side of the plane there are five other large septa which pass from the side of the fossa to the margin.

These ten septa together with the two directive septa constitute the primary twelve septa of the coral and were the earliest septa to be formed in the development of the coral. The other septa have been formed later and interposed between the primaries in series, and thus we have secondaries, tertiaries, and quaternaries, etc., each series of septa being smaller than the preceding series and approaching less closely to the fossa. The determination of the series of septa in any specimen of good size requires the exercise

of a great deal of care and patience, and many difficulties have usually to be overcome owing to irregularities in growth.

It cannot be expected that any one would care to determine the orders of sequence of the septa unless he were specially interested in the group, but it is of importance for the student of corals to understand that the general principles of septal sequence are manifest in *Fungia* with its hundreds of septa, as in other Madreporarian corals with septa that can be more easily recognised and counted.

The most important point to notice in the study of the septa of this coral, however, is the presence of the synaptacula. It is important because the synaptacula form one of the characteristic features of the family and because in *Fungia* they are larger and more easily studied than in any other genus. The synaptacula are bars of coral substance that pass from one septum to another at regular intervals, binding the septa together and giving rigidity and strength to the coral as a whole. As a rule the synaptacula do not appear near the upper regions of the septa but are more or less hidden in the depths of the interseptal spaces. They can usually be seen, if the specimen is not too massive, by holding the coral in front of a strong light, or, for more careful study, by filing down the septa of a part of a spare specimen until they are reached.

It may be an open question whether in *Fungia* there is a true columella. The fossa is usually deep and at the bottom of it there is a plexus of calcareous trabeculae which may be regarded as a rudimentary columella.

The single large polyp that gives rise to this coral has a slit-shaped mouth in the centre of the disc above the fossa, and it is surrounded by an enormous number of long tentacles slightly inflated at the extremity. It might seem at first sight that the tentacles are indefinite in number and irregularly scattered over the surface of the disc, but a careful study of the hard and soft parts has shown that each tentacle is situated on a slight elevation close to the innermost edge of a septum and that consequently the tentacles have the same orderly sequence as the septa and are arranged in regular cycles. The soft fleshy body wall of the polyp covers

the whole of the under surface of the coral, in a healthy specimen.

The mouth leads into a short stomodaeum or throat, and between the throat and the body wall there are as many mesenteries as there are septa. The pair of mesenteries situated at the angles of the mouth, one mesentery on each side of the directive septa, are the directive mesenteries. The other mesenteries are situated between the lateral septa and are either complete or incomplete, the primary and secondary mesenteries extending the whole distance from the margin to the throat, the others extending only a part of the distance from the margin to the throat, according to the series to which they belong. In the lower parts of the disc the mesenteries are perforated by the synaptacula.

It will be seen from the account given above that the polyp of a *Fungia* is an ordinary Madreporarian polyp and presents no feature of an extraordinary kind except its great size and the perforation of the mesenteries by the synaptacula.

The colour of the polyps is very variable, some specimens being described as green and others as brown, but the inflated tips of the tentacles are white.

No account of the structure of *Fungia* would be satisfactory without reference to some of the principal variations from the types that have been described.

On some reefs the symmetrically round disc shape is rare, most of the specimens being elongated in the directive diameter so as to become oval. Other variations may be found in which the fossa is not elongated but an almost circular pit, or the upper surface very convex or the outline quite irregular. In some specimens the thecal wall as seen between the costae is perforated.¹

Variations in colour have already been referred to, but there seems to be also some difference between species or perhaps simple variations in the length of the tentacles. Rumphius refers to them as little blisters ("blaasjes"), and Dana says the tentacles are small and rudimentary, but the excellent photographs of the living polyp by Saville Kent,

¹ Specimens showing an imperforate thecal wall were formerly placed in a separate genus *Cycloseris*.

and the observations and drawings of other authors, prove that in some cases, at least, the tentacles are of considerable length, like those of the common British sea-anemone *Tealia*.

It has been said that *Fungia* is free, and so it is in the adult condition when it is large and conspicuous; but in the early stages of its development it is fixed by a base of attachment to a rock or to another coral. In the young fixed stage *Fungia* is very much like a *Caryophyllia*. It



FIG. 24.—Young stalked form of *Fungia*. R., a part of the rock to which it is attached. S., the stalk showing the line when fracture is about to take place. Nat. size.

has an irregular base of attachment, an imperforate thecal wall, and twelve primary septa. This stage is called the Trophozoid. After a time the free edge of the Trophozoid expands and, becoming wider and wider, gives rise to a second stage with a form like the mouth of a trumpet. When the expanded part of the coral, the Anthocyathus, at this stage has reached a certain size—the septa having increased in number as it has grown—it breaks off and becomes the free *Fungia* (Fig. 24). The stalk or basal part, called the Anthocaulus, remains behind and gives rise to another

Fungia in the same way or, by lateral budding, may give rise to several young Fungias.

This very remarkable and unique method of reproduction is of very great interest because the detachment of the Anthocyathus from the Trophozoid seems to be a method of reproduction by fission quite unlike the fission seen in other corals. It is not vertical, but horizontal or transverse fission. It is different also from ordinary fission in the respect that the products are unequal and unlike each other. The lateral buds that are formed on the Anthocaulus after the Anthocyathus has broken off seem to be formed by gemmation in the ordinary way; so that in Fungia we have reproduction by gemmation as well as by this extraordinary method of fission. It is probable that gemmation also occurs in the free adult stages, because, when the under sides of a number of large Fungias are examined, a few young forms are occasionally found attached to the thecal walls. This was observed by Ellis, who wrote, "In many curious collections, such as those of the Duchess Dowager of Portland and of Dr. Fothergill, there are many young ones (of *Madrepora fungites*) adhering to the old ones with large rising lamellae as in the old ones."¹ The development of these young ones has recently been described by Boschma, who has proved that they are produced by gemmation and not from free larvae.²

But that is not the whole story, for in some species, formerly placed in a separate genus *Diaseris*, the disc-shaped free coral, when it has reached a certain size, divides by vertical fission into four quadrants, and each survives to restore in the course of time by unequal growth the three missing quadrants of its body.

Fungia has been shown to be a solitary coral, but its corallum has a very similar appearance to the coralla of a series of genera which are really compound corals.

HALOMITRA.—The first of this series is the genus *Halomitra*, originally described by Rumphius under the name

¹ Ellis, *Zoophytes*, p. 153.

² H. Boschma, *Proc. Konink. Akad. Wet. Amsterdam*, xxvi., 1923.

Mitra polonica, or Polish cap, on account of its cup or cap shape.

Although many variations in its exact form are now known, the most characteristic specimens are deeply concave on the under surface, the area round the central fossa being raised on the top of the convex upper surface. The numerous septa passing radially from the fossa to the circumference of the coral are not all straight and continuous, as they are in *Fungia*, but some of them appear to be deeply indented in their course, forming pit-like depressions to which neighbouring septa are inclined and from which new septa arise.

These pits represent the position of a series of small secondary polyps arranged more or less irregularly in a ring or series of rings round the central polyp of the fossa.

HERPETOLITHA¹ is the next genus in this series, and can usually be distinguished from the other genera by its elongated form, which is sometimes bent in a serpentine fashion (Fig. 25). Running along the middle of the upper surface is a long deep fossular groove in which the septa appear to radiate not from one centre but from a number of distinct centres, and the septa on each side of the groove are interrupted in the same manner as they are in *Halomitra* by a large number of irregularly scattered pits.

In a figure of a living *Herpetolitha* given many years ago by Dana it is shown that in the flesh that covers the median groove there is a series of mouths, each one surrounded by a patch of bright green colour in marked contrast to the brown colour of the tentacles and other parts of the coral polyp, and similarly that in each of the lateral pits there is a little mouth surrounded by a green patch and a circle of brown tentacles. We have in *Herpetolitha*, therefore, an advance on the structure of *Halomitra* in that the corallum is constructed by a number of larger polyps in the median fossa and a greater number of smaller polyps situated laterally.

Specimens of this genus sometimes reach a very considerable size. There is a specimen in the Manchester Museum 13 inches in length and $3\frac{1}{2}$ inches in width, which

¹ Frequently spelt *Herpolitha* by authors.



FIG. 23.—Herpetolitha, showing the elongated fossa and the cavities at the sides which are occupied by small polyps. $\frac{2}{3}$ nat. size.

weighs a little over 2 lb., and no doubt larger specimens than this have been found.

The development of *Herpetolitha* has not yet been fully worked out, but the presence of a distinct scar on the under side of small specimens leaves no doubt that in the early stages it is provided with a stalk of attachment as in *Fungia*.

POLYPHYLLIA.—The final stage in this series of genera is found in *Polyphyllia*, in which the sharp distinction between calices of the median groove and the lateral calices tends to become lost, and the corallum seems to be composed

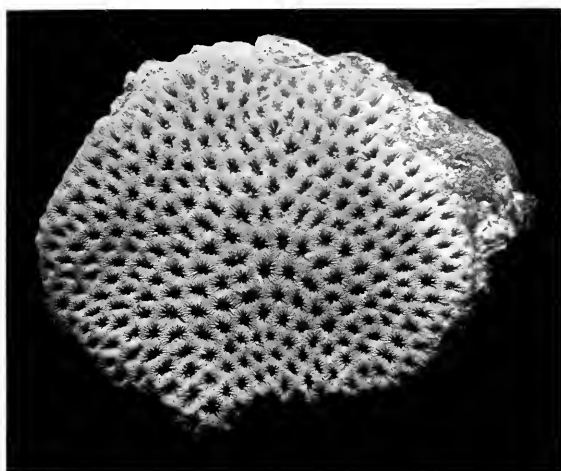


FIG. 26.—*Siderastraea radians*. West Indies. A small specimen. Nat. size.

of a number of very irregular and incomplete calices of various sizes.

All these genera, except *Fungia*, are confined to shallow water of the tropical Indo-Pacific regions.

The genera of the family which have been described above are all free in the adult stage, those that are still to be considered are permanently attached to some other coral or rock.

SIDERASTRAEA.—The genus *Siderastraea* (Fig. 26) includes a number of corals which are very abundant on the West Indian reefs and occur also in the Indian Ocean and

elsewhere in tropical seas. In habit they resemble some of the more typical *Astraeid* corals, being massive, dome-shaped, lobate, or encrusting, and the surface is honeycombed with small close-set calices without any intervening coenosteum. There can be no doubt that the old generic name, *Astraea* or Star-coral, was first given to a member of this genus, and it seems an unhappy fate for it to be removed to another family than that to which it gave the family name. A detailed examination of the structure of the coral, however, proves quite conclusively that it is more closely related to *Fungiidae* than to the *Astraeidae*, but it differs from the *Fungiidae* sufficiently to justify the course, which many authors prefer, of placing it, together with a large number of extinct genera, in a separate family or sub-family called the *Plesio-fungiidae*.

The calices are usually quite small (*i.e.* 4-6 mm. in diameter), and each calyx is separated from its neighbours by a common thecal wall which is rounded above and ridged by the outer edges of the septa. The septa are numerous (36-48) and arranged in several series of magnitude, as in *Fungia*, but it is a characteristic feature that they are, relatively to the size of the calyx, very thick, so that the interseptal spaces are very narrow. The free edges and the sides of the septa are beset with many coarse granular tubercles, and in the lower parts of the septa some of the tubercles of adjacent septa meet to form true synapticula (Fig. 27).

It is perhaps of some importance to note that in *Siderastraea* neither the septa nor the thecal walls are ever perforated by holes, so that it is strictly an imperforate coral. The calyx is considerably depressed in the middle, and from the bottom of the central pit there rises a short papillose or smooth but perfectly distinct columella.

The method of asexual reproduction is very difficult to understand by the study of the dried corallum. Small young calices can be seen interposed in the angles between the older ones and appear to arise from the common thecal wall. In some cases it might be supposed that the young calyx has arisen from an older one by a process of fission,

but the researches of Duerden have shown that the process is only a special form of gemmation which he calls "fissiparous gemmation."

The appearance of a living colony of a West Indian *Siderastraea* has also been fully described by Duerden.¹ According to this author the small expanded polyps (5-6 mm. in diameter) are outlined by a narrow polygonal groove of a lighter colour than the rest of the polyp wall. This groove corresponds with the upper limit of the common calicinal wall between the polyps. The expanded polyps

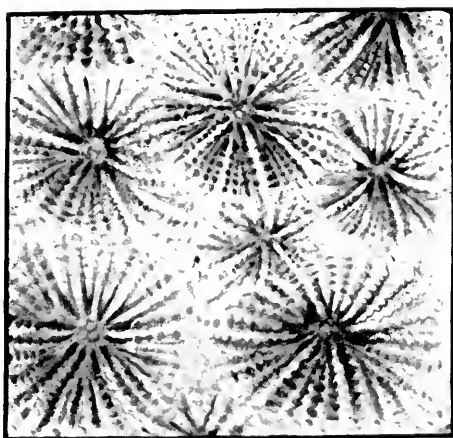


FIG. 27.—*Siderastraea siderea*. A small portion of the surface of a specimen from the West Indies, showing the calices, septa, and synapticula. $\times 6$ diams.

rarely assume a cylindrical form with a flattened terminal disc, like most coral polyps, but exhibit merely a dome-like elevation of the walls over the calyx (2 or 3 mm. high). In contraction they are not covered over by a fold of the body wall, but, as in *Fungia*, the tissues and the tentacles sink down as far as possible into the spaces between the septa. The tentacles are wide apart and occupy a broad band round the oral disc. When fully expanded they consist of a broad basal part which, in most members of the

¹ J. E. Duerden, "The Coral *Siderastraea*," *Carnegie Publications of Washington*, 1904.

inner cycles, becomes bifurcated, each branch terminating in a knob armed with batteries of nematocysts; the other tentacles are simply digitate. The colour of the polyps varies according to the position of the colony on the reefs. If they are not exposed to the sun they may be colourless, but elsewhere they vary from light to dark brown. The oral disc may show radial streaks of velvety green and the angles of the mouth and the knobs of the tentacles are white.

The following genera belong to the section of the family sometimes called the Lophoseridae.

AGARICIA.—This coral forms colonies which are usually foliaceous in growth, the calices arranged in irregular concentric rows on the upper or, more rarely, on both sides of the leaves (Fig. 28). The rows of calices are separated by prominent thecal ridges. The calices are small, 3-4 mm. in diameter. The septa are numerous, as in other Fungiidae, but do not extend from the margin as close to the centre of the calyx as they do in *Siderastraea*, and consequently leave a deeper and wider oral pit. The sides and margins of the septa are profusely tuberculate, and in the depths of the interseptal spaces the tubercles meet to form synaptacula. Asexual reproduction is by fission.

Agaricia seems to be a widespread but not very common coral on both East and West Indian coral reefs. In Jamaica, according to Duerden, the colonies occur in shady places at a depth of from 3 to 4 feet downwards, and are of a conspicuous bright reddish-brown colour. The tentacles are rudimentary, from ten to eighteen in number, and widely separated. In the state of contraction this coral resembles other members of the family in that the polyp walls are not folded over the oral disc. In the state of expansion, emerald green circles can be seen surrounding the mouth on the oral disc.

As in many other corals in which asexual reproduction is by fission, there are no directive mesenteries in the polyps.

PAVONA.—The genus *Pavona*, which belongs to the same group as *Agaricia*, does not occur in the West Indies but is fairly common on some of the Indian Ocean and Pacific reefs. It differs from *Agaricia* in having much less prominent



FIG. 28.—*Agaricia*. Indian Ocean. Nat. size.

ridges, so that the surface is relatively smooth and striated instead of being rough and ridged.

PACHYSERIS.—The last of these genera that need be mentioned here is *Pachyseris*, which shows the most extreme form of modification of the original system of distinct calices (Fig. 29).

The coral is in the form of large rather thin cordate or more irregular fronds attached by a short thick stem. The under surface is a thin imperforate plate. The upper surface consists of a series of concentric parallel ridges and valleys, the valleys being traversed by an immense number of rela-

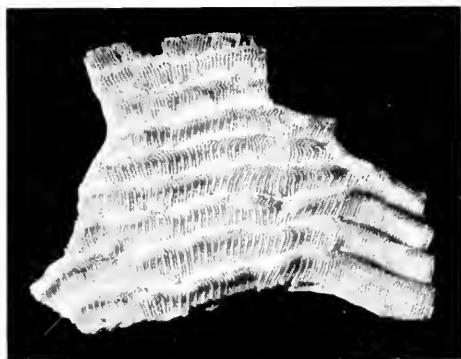


FIG. 29.—*Pachyseris*. A part of a large frond showing the calices completely merged into parallel ridges and grooves. $\times 2$ diams.

tively thick and parallel septa. There is no indication whatever of any distribution of these septa into discrete calical areas. *Pachyseris* is a widely distributed but not very common coral found in shallow water in the tropical Indian and Pacific Oceans.

FAMILY 5. EUPSAMMIIDAE

This family can readily be distinguished from the preceding families by the complete perforation of the walls of the calices and, in most genera, of the septa as well. It was formerly placed in the old division of *Madreporaria* known as the *Perforata*, but in the general structure of both

the corallum and the polyps it is more nearly related to the Imperforata.

In all the genera there are more than twelve septa, as in most of the Imperforata, and a special character of the family is that some of the septa fuse along their inner margins to form a number of triangular interseptal spaces. In most of the genera the septa and thecal walls are armed with spines or small tubercles, but only in rare cases do they join to form synapticula. The family includes both simple and colonial forms.

BALANOPHYLLIA.—The little coral called by Gosse¹ “the scarlet and gold star coral” (*Balanophyllia regia*) is a representative of the solitary Eupsammiidae that is found in British seas. It was found by that author attached to the rock-pools at low-tide near Ilfracombe, associated with the Devonshire cup coral (*Caryophyllia smithii*, Fig. 2, p. 26). It has since been found in other localities off the coasts of Devonshire and Cornwall, but it is still far from being one of the common objects of the seashore.

The dried corallum (6-8 mm. in height and diameter) can readily be distinguished from that of *Caryophyllia* by the two Eupsammiid characters—the perforation of the walls and septa and the confluence of some of the septa to form triangular interseptal spaces with their bases on the thecal wall. The polyp is like a little sea-anemone with a mouth situated on a cone rising from the centre of the oral disc, and the margin of the disc is provided with a single cycle of about fifty long tentacles. Gosse described the tentacles as “conical, obtusely pointed, without terminal knobs,” and there is little doubt that this is a good description of what he saw in the rock-pools at low tide. But de Lacaze-Duthiers, who studied this species, from the coast of France, alive in a small aquarium, says that when fully expanded the tentacles are long and finger-like, and terminate in little knobs as in *Caryophyllia*. As in the latter coral also, the sides of the tentacles are armed with batteries of nematocysts which have the appearance of little warts.

The colours of the Devonshire specimens were described

¹ P. H. Gosse, *British Sea Anemones and Corals*, 1860, p. 343.

by Gosse as vivid scarlet in the adults, orange in the young individuals, opaque; the tentacles gamboge yellow, the hue residing only in the warts.

ENDOPACHYS.—The genus *Endopachys* (Fig. 30) is still a rarity in museums, and has not been found in any locality in large numbers. It is of some special interest, however, because in size and in form it closely resembles the Turbinoliid coral *Flabellum*, and, like *Flabellum*, it is attached to a stone or shell when it is young, but becomes free by fracture of the base in the later stages of its growth. A critical examination of a specimen, however, shows that



FIG. 30.—*Endopachys grayi* with a marginal bud. Persian Gulf, 55 fathoms. Nat. size.

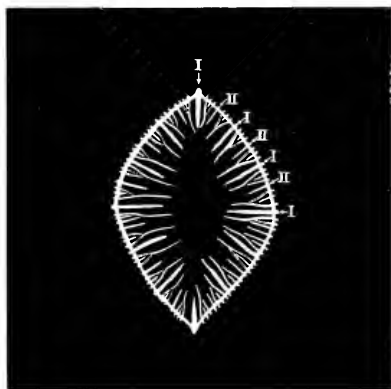


FIG. 31.—Diagram to illustrate the septal arrangement of *Endopachys*. I, I, primary septa; II, II, secondary septa.

it is thoroughly perforate and that the septa have an Eupsammiid arrangement (Fig. 31). One or two specimens only have been found in such distant localities as the Persian Gulf, Hawaii, the Malay Archipelago, and Manilla, but the genus is represented by several species, and is very abundant in some of the Eocene deposits of the United States of America.

Endopachys and *Flabellum* present us with an excellent example of the principle known as "convergence in nature." There can be no doubt that they are not closely related, and

we are justified in placing them in separate families, but in order to become adapted to the same or similar mode of life they have adopted the same external form and a similar change in habit at the same time of life.

Both genera are usually found on a gravelly or sandy bottom, in contrast to most corals, which are found on a hard bottom. When they are very small they can be supported on a small shell or stone, but when they are larger and heavier than the stone there is a tendency for them to be overbalanced and smothered in the gravel. The only way to overcome this danger is to become detached from the stone and support themselves as best they can as free corals. We have unfortunately no record of observation made on the living coral, and it is not possible to hazard a guess as to how this is done, but there can be little doubt that the peculiar compressed cone shape and the variable wing-like side processes in both genera are special adaptations for this purpose.

Another point of interest about *Endopachys* is that it is probably one of the corals on the verge of extinction. It may have been very abundant in Eocene and later times, and thus have become spread over a wide area in suitable localities, but is now very rare, and shows the common attribute of many rare things, a wide but discontinuous geographical distribution.

HETEROPSAMMIA.—Another example of convergence, but convergence of a different kind, is seen in the Eupsammiid coral *Heteropsammia* (Fig. 32). This coral is either solitary or forms small colonies of two or three polyps by fission, but it is very frequently free and associated in its freedom with a small sipunculid worm like the Turbinoliid coral *Heterocyathus*.

Both these corals are found on sandy bottoms, sometimes in the Indian Ocean, together or in close proximity, and they have found out quite independently the same dodge for maintaining an upright position in the shifting sand.

DENDROPHYLLIA.—*D. ramea* is a large branching coral with a general form not unlike that of *Lophohelia*. And just as the perforate solitary *Balanophyllia* is sometimes found

associated with the imperforate Caryophyllia, so the compound Dendrophyllia is found associated with Lophohelia.

Dendrophyllia has a very wide distribution. The most familiar species, *D. ramea*, is found in moderately deep water in the Mediterranean Sea and in the Atlantic Ocean, and other species occur in shallow water on the reefs of the tropical Indian and Pacific Oceans. *D. ramea* sometimes attains to an enormous size. De Lacaze-Duthiers records the capture, by the fishermen of La Calle in Algeria, of a block of this coral a cubic metre in size. It also shows a complex amalgamation of branches similar to that described and figured for *Lophohelia prolifera* (see Fig. 5, p. 28).

A critical examination of the method of growth of Dendrophyllia shows that it is essentially different from that of Lophohelia. The great branches of Dendrophyllia are in reality enormous calices with very thick walls, on which the smaller branches and calices have arisen by lateral or thecal gemmation. The calices vary a great deal in size, as in all these corals, but in a typical medium-sized specimen in the Manchester Museum they are about 10-15 mm. in diameter. Each calyx shows a deep and wide cavity, at the bottom of which a more or less well-developed columella may be seen. The septa are thin, barely exsert, not very wide, and those of the young cycles bend towards and fuse with the older septa as in other Eupsammiids.

The only account we possess of the polyps of a European species of Dendrophyllia is that of *D. cornigera*, from the Golfe du Lion, by de Lacaze-Duthiers, who says that the colour is of a beautiful yellow-gold, the mouth being surrounded by a band of orange-red colour. The tentacles are very long and of equal size and are dotted with little yellow spots.



FIG. 32.—*Heteropsammia*. Indian Ocean, 30 fathoms. Upper surface on the right, showing the calyx. Under surface on the left, showing the aperture formed by the sipunculid worm. Nat. size.

In his description of the species *Dendrophyllia Willeyi*, on the reefs of the Cocos Islands, Dr. Wood-Jones says that "when the colony consists of one or two polyps it is coloured bright chrome yellow, when older it is bright vermilion, but at all times it has an iridescence resembling solutions of eosin."

ASTROIDES.—Another Eupsammiid coral that has become familiar to us is the *Astroides calicularis* of the Mediterranean Sea (Fig. 33). This is the coral to which Boccone gave the poetic name "la pierre étoilée." It usually forms small

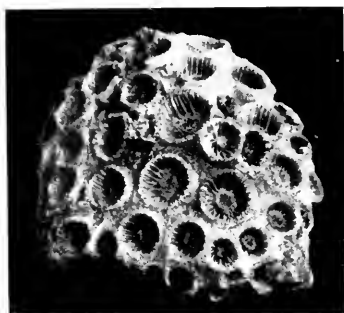


FIG. 33.—*Astroides calicularis*. Mediterranean Sea. $\frac{3}{4}$ nat. size.

encrusting colonies composed of a number of calices about 7-8 mm. in diameter and 4 mm. in height separated from one another by a sparse coenosteum. The cavity of the calyx is wide and deep, and rising from the centre there is a well-developed conical trabecular columella. The septa of a full-grown calyx are forty-eight in number and arranged in four cycles. There is less regular and complete confluence

of the third and fourth cycles of septa in *Astroides* than is usual in the genera of this family, but some confluence does occur in nearly all the calices.

The polyps have a bright orange colour, and when fully expanded stand up from the calices as tall columns terminating in an oral disc surrounded by a crown of forty-eight simple digitate tentacles.

This coral is of special interest to students of coral morphology, as it was the subject of the important researches of de Lacaze-Duthiers and von Koch which laid the foundations of our knowledge of the embryology and the development of the skeletal structures in the Madreporaria.

CHAPTER IV

MADREPORARIAN CORALS (*continued*)

"Die Corallenthiere sind nicht bloss für Naturbeschreibung und Naturgeschichte im engeren Sinne merkwürdig, sie gehören zu den zahlreichsten, auffallendsten, unbekanntesten und am einflussreichsten Formen des organischen Lebens"—H. EHRENBERG, *Abh. Akad. Wiss.*, Berlin, 1834.

FAMILY 6. SERIATOPORIDAE

THIS family contains only three recent genera—*Seriatopora*, *Pocillopora*, and *Stylophora*. They are found, commonly but not abundantly, on most of the coral reefs of the world except those of the West Indies. The family is of considerable interest from many points of view, and it is also well defined and easily recognised. There has been a great deal of difficulty in placing it in its proper position among the families of the Madreporarian corals, as in some respects it seems to have affinities with the old group of imperforate corals, in other respects with perforate corals, and again in the presence of very definite tabulae it agrees with some of the extinct corals.

As the most striking feature of the anatomy of the two genera is the definite restriction of the number of mesenteries and of septa, in the full-grown zooid, to twelve, a feature in which the family differs from all those that have been previously described, and agrees with the *Madreporidae* and *Poritidae*, the affinities are probably closer with the perforate corals than with the imperforate.

Seriatopora and *Pocillopora* have the following characters in common. They are colonial corals, forming profusely ramified shrubby or bushy growths reaching a size

of a foot or two in diameter. The surface of the branches is rough owing to the presence of a number of minute spines or tubercles on the surface, and the calices are very small, their appearance being represented by holes or pits usually flush with the surface. There is of course some variation in the size of the calices, but it may be found that in a large collection of specimens the average diameter of the calices at the margin is less than 1 mm.

These characters can be easily determined, but there are some very important ones which require careful observation and manipulation of the light to be clearly demonstrated.



FIG. 34.—*Seriatopora*. A few terminal branches of a large colony. Nat. size.

In many dried specimens there seem to be no septa at all even when the calices are examined with a magnifying glass. This may be due either to the presence of the dried remains of the polyp tissues, which obscures the septa, or to the calyx examined being old and water-worn with the septa partly destroyed. To examine the septa, smaller terminal branches should be thoroughly cleaned by boiling in 5 per cent. potash for some time and

then dried and examined in a good light, on a black ground, with a powerful lens or low-power microscope. It is only by such means that it can be definitely ascertained that there are nearly always twelve small septa, of which six may be complete and six incomplete. Moreover, of the six complete septa two are larger than the others and form a pronounced ridge on the floor of the cup. These two septa are the directive septa and they always lie in a plain parallel with the axis of the branch.

The next two points to determine require the examination of a transverse section of a thick branch or the exposed surface of a freshly made fracture. It may then be seen

that each calyx is shut off by a thin tabula from a little chamber below it, and this again by another thin tabula from another chamber of the same diameter, or, to put the same thing in another way, the corallum is perforated by a number of radial tubes which are divided by thin plates of coral substance into a series of closed chambers, of which the outermost one is freely open to the surface and forms the calyx. The Seriatoporidae are in fact Tabulate corals.

Further, the same sections or fractures will show that apart from these chambers the corallum is quite solid and there are no communications between one set of chambers and another. They are in fact imperforate corals.

Our knowledge of the characters of the polyps is based on the study of only a few specimens, but there seems to be no doubt that as a rule the polyps are provided with twelve short tentacles and twelve mesenteries, of which two pairs are directive mesenteries. The tentacles of a species of *Seriatopora* described by Fowler are capitate in form and show the very remarkable and, in *Madreporaria*, unique character of being introverted during retraction.

The polyps are connected with one another by a thin and entirely superficial layer of coenosarc supported by the spines of the coenosteum, and in this runs a delicate network of nutritive canals. This elaborate system of canals, running entirely superficially to the coenosteum, is similar to the system of canals which connect the polyps in some of the perforate corals, such as *Madrepore* and *Dendrophyllia*, but in the case of the latter is continued downwards into the perforations which traverse the coenosteum.

In the description of corals, pathological conditions are not usually mentioned, and considerations of time and space often render such a course imperative. But in this family there is one kind of pathological change which is of exceptional interest. Like other corals, *Pocillopora* and *Seriatopora* may be attacked by certain barnacles, worms, and molluscs in such a way as to modify in some way the normal method of growth, but they are also liable to what may be

called a friendly association with a little crab (*Hapalocarcinus*).

When this crab is very small it settles down in the fork between two young branches and, by some kind of continuous irritation or stimulation, causes each branch to divide into a number of lateral but anastomosing branchlets which, spreading out on each side of the fork like a fan, eventually converge above and form a cage in which the crab is imprisoned for life (Fig. 35).

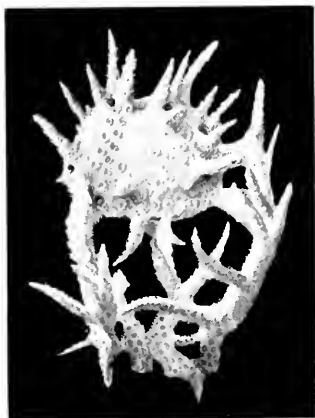


FIG. 35.—An example of *Seriatopora*, in which some of the branches have coalesced to form a gall for the crab *Hapalocarcinus*. Nat. size.

In some specimens a large number of these crab cages may be seen, and so far as can be judged by appearances they do not seem to interfere with the general well-being of the colony as a whole. It may seem to be a bold assertion to make, that imprisonment for life is beneficial to any living creature, but as the adult female *Hapalocarcinus* is never found anywhere except in one of these cages it may be presumed that, if she has a mind, she prefers it. At any rate it is certain that confined to this prison she can obtain sufficient food for her nourishment and can successfully reproduce her kind.

The special point of interest for the student of corals to consider is why these crab cages are so frequently found in these two genera, *Pocillopora* and *Seriatopora*, and not in others. The only recorded instance of a crab cage of this kind on a coral of another genus is in a specimen of *Millepora* from the West Indies, now in the Public Museum at Liverpool, but they are not known to occur on any species of *Madrepora*, *Oculina*, or other corals with a similar method of branching. Is there some special scent or flavour in the *Seriatoporidae* which attracts the crabs to these corals? This is a question to which no satisfactory answer can be given at present.

A few words must now be added on the difference between the two genera.

SERIATOPORA.—*Seriatopora* can usually be distinguished at once from *Pocillopora* by its slender and sharply pointed terminal branches (Fig. 34). The calices are arranged in longitudinal rows on all sides of the branches and in some species show a margin raised above the level of the coenosteum. The two directive septa form a prominent ridge on the floor of the cup, and this ridge is always parallel with the axis of the branch. It may be a matter of dispute whether the middle part of this ridge should be called the columella, but the most reasonable point of view seems to be that there is no columella. The other septa are often very rudimentary and difficult to see. In some specimens there are only four and in others eight, or if we count the two directive septa, six or twelve in all.

The colour of living *Seriatopora* on the reefs is usually pink, but yellow varieties have been found. In some cases the polyps appear as brown spots on the branches.

POCILLOPORA.—In *Pocillopora* the method of branching is coarser and more irregular than in *Seriatopora*, and the terminal branches are thick and blunt at the apex, never being drawn out into fine points. The surface of the branches is very rough and in many species raised into a series of little mounds or verrucae. The calices are very numerous, and as compared with *Seriatopora* very close together, so that in many places they are actually in contact with one another. The study of the septa of these minute calices is beset with even greater difficulties than in *Seriatopora*, because in many specimens their cavities are filled up with a chalky deposit (stereoplasm), which completely hides the structures buried in it and cannot be removed by the ordinary cleaning reagents. However, when a terminal branch of a good specimen is examined in a strong light with a lens, a ridge formed by the directive septa and parallel with the axis of the branch can usually be made out. A more detailed examination of this ridge with a higher power, however, shows that in the middle of it there is usually a definite but small papilliform columella. In addition to the

two directive septa there are four other large septa alternating with six smaller ones. The colour of living colonies of *Pocillopora* is usually green, sometimes "a most brilliant dark green" (Gardiner). Other colonies are colourless or pink.

STYLOPHORA.—The genus *Stylophora* (Fig. 36) is not an uncommon coral on the reefs of the Indian and Pacific Oceans, and calls for a few words of comment, because, in some respects, it has a superficial resemblance to varieties of the Hydrozoan genus *Stylaster* (p. 153).

As the name suggests, the most characteristic feature it exhibits is the prominent pillar-like columella (Fig. 37), which stands up in the centre of the calyx, and as this feature is combined with that of narrow and usually rather thick septa the calyx has some resemblance to a pore cycle of one of the *Stylasterina*. A critical examination of a calyx shows, however, that the spaces between the septa are not pierced by dactylopores and that the six thick primary septa are supplemented by six thinner rudimentary ones.



FIG. 36.—*Stylophora*. The terminal branch of a colony from the Indian Ocean. $\times 2$ diams.

Stylophora is undoubtedly a Madreporarian coral, but the authorities are not agreed as to its exact systematic position and generally place it with *Madracis* in a separate family—the *Stylophoridae*; but it agrees so closely in many important characters with *Seriatopora* that there seems to be no sufficient reason for excluding it from the family *Seriatoporidae*.

The form of the corallum is usually arborescent, the branches ending in thick blunt points, but sometimes it is palmate or encrusting. The substance is hard and compact except in the axis of the larger branches, where it becomes porous, and the ends of the growing points, where it is perforated by calicular pores.

The small calices are separated by a considerable amount of coenenchym, which is adorned with a great number of small blunt tubercles giving it a granular appearance. In some specimens these tubercles fuse to form ridges. The

calices are about 1 mm. in diameter and project slightly and obliquely from the surface so that the disc of the polyps when expanded is directed upwards towards the apex of the branch on which they are situated. There are six thick but rather narrow primary septa, and in some calices six thinner secondary septa can be seen. The most prominent feature of the calyx is the strong pillar-like columella.

The cavity of the calyx is shallow and shut off below by a thin calcareous plate. Below this plate the corallum is pierced by a long cylindrical pore divided into a number of chambers by transverse tabulae (Fig. 37). According to some authors the endotheca is in the form of irregular dissepiments, and possibly it varies in different species or in different conditions, but in the specimen from which Fig. 37 was drawn the pores were distinctly tabulate.

The polyps of *Stylophora* possess twelve capitate tentacles, six larger and six smaller; and there are almost invariably twelve mesenteries, of which two pairs are directives. The polyps are connected with one another by a thin coenosarc, which lies entirely above the coenosteum, and in its lower layer there is a network of canals running between the tubercles as in *Seriatopora*.

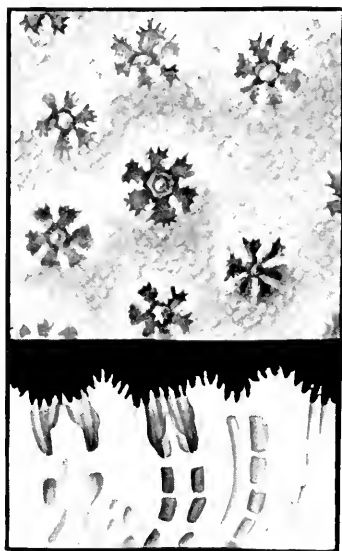


FIG. 37. — *Stylophora*. Upper figure showing the surface of the coral. Lower figure showing the calices in vertical section. — circa 25 diams.

FAMILY 7. MADREPORIDAE

The corals belonging to this family constitute the most dominating feature of modern coral reefs, and probably contribute, by the activity of their polyps, a larger propor-

tion of the calcareous substance of which the reefs are composed than any other group of corals. They are, however, of comparatively recent origin, as they do not seem to have attained to any degree of importance as reef-builders until the later Tertiary times, when they overtook and replaced to a great extent the Astracidae and other groups of imperforate corals in the struggle for existence on the reefs. The cause of this change of dominance may be due partly to the rapidity of growth and partly to the extraordinary plasticity in form of the Madrepores as compared with other corals.

The construction of a perforated corallum requiring the secretion of a relatively small amount of calcium carbonate for a given surface of support for the polyps and the provision of an elaborate system of coenosarcular canals, usually crowded with active zooxanthellae, are characters which undoubtedly assist physiologically in rapid growth.

The complex of conditions which renders some coral reefs of the tropical seas more favourable for the growth of Madrepores and others less so is so intricate that it will prove to be a very difficult tangle to unravel. The mean temperature of the water, the violence of the breakers on the shore, the abundance and character of the food supply of microscopic organisms, and the chemical constitution of the sea-water are factors which, in varying combinations, determine whether a particular kind of coral shall predominate on a reef. On one reef may be found an abundance of Madrepores, on another Heliopores and Astracids, on another little more than a carpet of Lithothamnion or some other form of calcareous Alga; but taking the reefs of the world as a whole, there can be little doubt that the three genera, Madrepora, Porites, and Montipora, do maintain the premier position in abundance and in luxuriance of growth on the coral reefs of the present day.

It is in this family also that we find, in a more exaggerated form, perhaps, than in any other, the difficulty of dividing up the genera into specific groups.

The careful study of a single large colony or of a collection of specimens from the same locality reveals so much variety

in general form, in the size of the calices, and in other characters which are available for the determination of species, that the task of the conscientious systematist seems to be a hopeless one. No attempt can be made in these pages to help him.

But there is one consideration of this problem which is worth bearing in mind, and may be of more general interest. If we consider a large collection of specimens of a *Madrepora* from a given reef, we may regard the differences we observe between them to be due either to characters inherited by them from their parents or to the moulding and fashioning effects of external forces that have played upon them from the time when the ciliated larvae from which they have sprung first settled down upon a rock.

If it were possible for us to experiment by breeding Madreporae, as we breed mice or canaries, we could determine whether these differences are inherited or not. But at present the difficulties in the way of making pure cultures of these corals seem to be insuperable.

In the absence of such direct experimental evidence, which can alone decide the matter, it is open to us to hold the opinion that the variations are due to local environmental conditions, and on this assumption we may hold that in such a genus there has been no subdivision into a large number of distinct specific groups, but only one large and very variable species is represented.

This view has not been proved to be correct or incorrect, but if it is correct, then we have a species which shows extraordinary powers of adapting itself in various ways to the complex of local conditions, and it may be that this adaptability or plasticity, as it is sometimes called, is an important character in gaining for the species its predominance on the reefs.

The word madreporae¹ was first used by Imperato in 1599, and there can be little doubt that the coral which he called Madreporae was the Mediterranean coral now called *Dendro-*

¹ The word madreporae has been frequently translated "Mother stone" (*Porus matronalis*), but should be translated "Mother of stone." Cf. Ital. *Madrepérle* = Mother of pearl.

phyllia ramca. Marsigli and other writers of the early part of the seventeenth century extended the application of the word to other white stony corals, and thus it came to be given by Brown, in 1756, to a coral which can be definitely recognised as a specimen of a coral having the characters of the modern genus *Madrepora*. Brown's specimen came from Jamaica, and he called it "*Madrepora ramosa major muricata et stellata aperturis cavernarum minoribus depressa*." Most unfortunately Linnaeus, in his *Systema Naturae* (10th ed.), published in 1758, changed the name to *Millepora muricata*, but corrected the mistake in the twelfth edition of the same work and called it *Madrepora muricata*.

The generic name *Madrepora* was accepted and used in the important treatises on corals by Lamarck, Milne-Edwards and Haime, and in more modern times by Brook and Bernard, the authors of the magnificent British Museum Monographs on Madreporarian corals, and by many other naturalists. It has been declared, however, that in consequence of the blunder made by Linnaeus in 1758, the name *Madrepora* should be abandoned and the genus given the name *Acropora*, originally proposed by Oken in 1815. It would be, in my opinion, a most grievous mistake if this suggestion were universally adopted. The meaning of the word *Madrepora* has become so definitely fixed by all the great men of science who have studied and described the anatomy of the hard and soft parts, and the species and varieties of form found in the genus, that a change of name will only lead to confusion in our literature. No more mischievous and senseless example could be chosen to demonstrate the absurdity of strict adherence to the so-called Law of Priority than the proposed change of the name *Madrepora* to *Acropora*.

MADREPORA is probably the most widely distributed and most abundant of all the reef-building corals of the world. On many of the reefs of the Indo-Pacific regions specimens of the genus seem to form an almost continuous carpet of coral, extending for miles along the coast-line, and in many places the water at low tide just beyond the edge of the reefs is

filled with forests of the branches of specimens which are rooted on the rocks of the sea-bottom.¹

The specimens the naturalist finds exposed at low spring tide do not as a rule attain to the same gigantic proportions as the massive *Porites*, but the branching specimens in deeper water outside the reef must be often many feet in height, with main stems nearly a foot in diameter. Massive colonies twenty to thirty feet in length are also found in some localities.²

The genus is found both in the West Indies and in the Indo-Pacific Ocean, the limits of its geographical distribution being almost identical with that of the coral reefs of the world. The forms assumed by the colonies are so varied and so much influenced by the local conditions and surroundings that it is quite impossible to express in a few words all the possible varieties of shape that a colony of *Madrepora* may assume. There are, however, three types of construction which may be recognised in a large collection of these corals, known respectively as *Forma palmata*, *Forma prolifera*, and *Forma cervicornis*.

In *Forma palmata* the colony arises from a short, thick stem attached to its support by a spreading or encrusting base, and divides rapidly into a number of branches which ramify and anastomose to form a fan-shaped or leaf-like frond, erect, oblique, or at right angles to the stem from which it arises.

In *Forma prolifera* the branches arising from a short stem divide and ramify to form an irregular bush-like growth, with usually less anastomosing of the branches than in *Forma palmata*.

In *Forma cervicornis* there is usually a long, thick, erect main stem, from which large, irregular, lateral branches are given off, which subdivide and but rarely anastomose. This form has the popular name Stag's-horn coral.

There are many intermediate forms between these three types and others that are massive, lobate, encrusting or lamelliform, and seem to be quite distinct.

¹ See photographs in Saville-Kent's *Great Barrier Reef of Australia*.

² Reference may be made to the large specimens in the British Museum.

As the general form of the colony of *Madrepora* is so variable, it affords no characters by which the genus can be safely distinguished from others. A close examination of one of the terminal branches is necessary to find characters

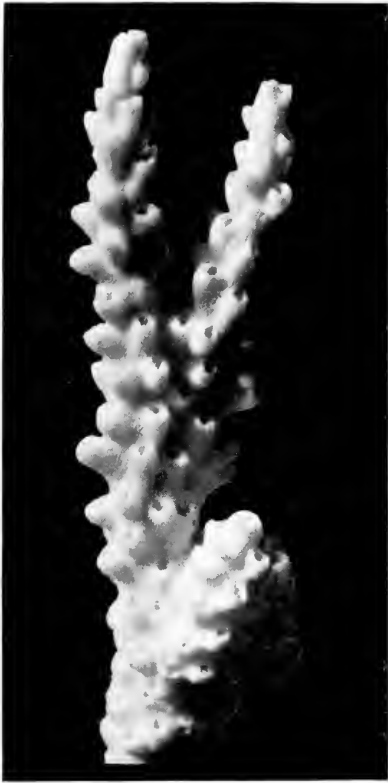


FIG. 38.—*Madrepora*. A terminal branch of a large colony of a Stag's-horn variety. 2 diams.

to be relied upon for this purpose, and fortunately these characters are so definite that it is nearly always quite an easy matter to determine for certain whether a given coral is or is not a member of the genus *Madrepora*.

Each terminal branch bears at its extremity a single large apical calyx, and below this a number of oblique calices of smaller size, arranged like a series of brackets on all sides of the branch. The smallest of these brackets are next to the apical calyx, the largest ones farthest away from it (Fig. 38). In some varieties the apical calyx is thick-walled and dome-shaped, so that the terminal branches are blunt or knob-like. The lateral calices have in these varieties more definitely

the appearance of being arranged in a radial manner round a very thick-walled axial calyx. Such varieties are sometimes regarded as belonging to the sub-generic groups *Isopora* and *Tylopora*. More rarely the axial calices are more or less laterally compressed and the lateral calices arranged principally in two series (sub-genus *Distichocyathus*).

If, now, the terminal branch of the commoner type of *Madrepora* be broken off and the surface of the fracture be examined, it will be found that in the axis of the branch there is a cavity traversed by radial septa which are continuous with the septa of the apical calyx.

It follows from this observation that the terminal branch represents the elongated calyx of a polyp which has given rise, by centrifugal gemmation, to a number of lateral polyps. The growth and fusion of the walls of the lateral polyps completely enshroud the calyx of the apical polyp which has given birth to them, and there is no common substance or coenosteum between them.

The number of septa in the lateral calices is usually six, and of these the two directive septa situated in planes which are radial to the axis of the branch are decidedly larger than the others and frequently meet in the centre of the calyx (Fig. 6, p. 32, DS). There is no columella. The apical calices have usually more than six septa, and in some cases the lateral calices have also more than six septa, but the number of septa seems to have reached its maximum when twelve have been formed, and calices with more than twelve septa are very rarely found. The character of the endotheca is very variable, but it is noteworthy that in some cases it takes the form of more or less regularly disposed tabulae.

The polyps of an expanded *Madrepora* appear to be of two distinct kinds. The apical polyps, projecting some 3 mm. beyond the apex of the branch, have only six long tentacles, and the lateral polyps, which project very little beyond the lip of the calyx, have twelve tentacles, six long and six short. But this does not seem to represent a true dimorphism such as we find in the polyps of many of the *Hydrozoa* and *Alcyonaria*, because at the rapidly growing margins of the colony many intermediate forms between the two kinds may be found, and it seems probable that a polyp of the twelve-tentacled kind may change into a polyp of the six-tentacled kind when it assumes the function of an apical polyp and starts the development of a new branch.

The tentacles seem to vary a good deal in character. Sometimes they are simply digitiform, sometimes they

terminate in a swollen apex and are capitate. Sometimes they are marked with white spots representing batteries of nematocysts, sometimes these spots are not noticeable. In retraction the tentacles may be introverted, but there is not sufficient evidence to prove that this is always the case.

The number of mesenteries is nearly always twelve in a full-grown polyp, and every polyp has two pairs of directive mesenteries (Fig. 6, III, III, and IV, IV, p. 32).

In some polyps additional mesenteries are formed in a manner which seems to be peculiar to *Madrepora*, *Porites*, and possibly some of their allies. Instead of being added in unilateral pairs right and left of the directive mesenteries, as they are in the *Astracidae*, they are added in bilateral pairs within the space between the two directives of a single pair of directives (Figs. 9 and 10, p. 35).

The colours of living *Madrepores* are so varied on different reefs and on different places on the same reef that it is difficult to make a general statement on the subject which can be of any value for the collector.

According to Duerden the colours of the Jamaican *Madreporas* vary but little. Colonies as a whole are lighter or darker shades of brown, becoming green, yellow, or orange. According to Saville-Kent, the different varieties of *Madrepora* on the Great Barrier Reef exhibit almost every possible colour variety from pale yellow through shades of green, pink, and brown to lilac and blue. On the coral reefs of a small island off the coast of Celebes, the *Madrepores* on one side of the island, which was more exposed to the surf, seemed to be uniformly brown, but in the calmer waters of the other side of the island there was much greater variety, the lilacs, bright greens, and yellows predominating. One of the most striking colour features of these corals is the brightness of the colours of the points of the branches. When seen from a boat through the clear sea-water on a bright, sunny day, these emerald green, pale yellow, lilac, or sometimes white terminal branchlets produce a most fascinating and startling effect even in a background that is itself a feast of brilliant colour schemes. When the tide falls,

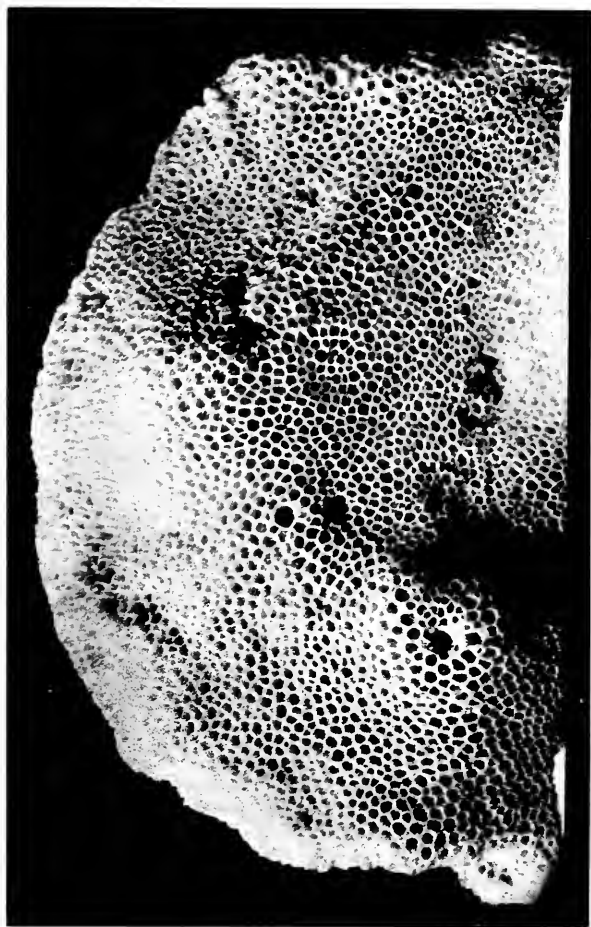


FIG. 39.—Porites. About nat. size.

however, and the corals are exposed for a time to the sun, the brilliancy to a great extent disappears, and a uniform dullness of brown and yellow seems to prevail.

PORITES.—The genus *Porites* is another very important reef-building coral widely distributed in the tropical seas of the Old and New World. In some seas, blocks of *Porites* reach to an enormous size,¹ and appear to be the principal factors in the construction of the reefs, but in others the *Porites* rocks occupy a subordinate position to the colonies of *Madrepora*, and relatively small blocks of it are scattered about in more or less isolated positions.

The forms assumed by the large colonies are almost as varied in *Porites* as they are in *Madrepora*; but in *Porites* massive, spherical, lobate, and encrusting forms are more characteristic. Ramified forms are found, but the branches are generally thick and terminate in blunt knobs. The ramification is seldom profuse.

The surface of the corallum is seen to consist of a very large number of small calices with common pentagonal thecal walls (Fig. 39). There is no coenosteum between the calices. The septa are twelve in number and the directive septa are not usually distinguished from the others by their greater size. All the septa are so profusely perforated that each one has the appearance of a lattice work of trabeculae rather than that of a perforated lamina. On the free border of the septa there is a row of blunt spines, and on their inner side there is a cycle of pali. In the centre of the calyx a single spine represents a columella. At the base of the calyx the septa are often seen to be connected by syntapcula. The substance of the corallum below the surface has usually the appearance of a most intricate maze of trabeculae, but frequently the cavities become filled with stereoplasm and, less frequently, the trabeculae show a tabular arrangement.

The living polyps of *Porites* project but slightly from the calices. The tentacles are usually twelve in number, digitiform or acute in specimens in Jamaica (Duerden), or

¹ For example, the great mass of *Porites*, 30 to 40 feet in diameter, described and photographed by Saville-Kent.

distinctly capitate in Australian Barrier Reef specimens (Saville-Kent).

The arrangement of the mesenteries in *Porites* is very similar to that previously described in *Madrepora*, and the increase in the number of mesenteries also takes place by the addition of bilateral pairs in the space between the mesenteries of one pair of directives.

The colour of the *Porites* is very variable and often very brilliant. Duerden¹ writes that "*Porites astracoides* (of Jamaica) is one of the most gaily coloured of all the West Indian corals, and occurring in large masses often becomes an important constituent in determining the general coloration of the reefs. As a rule the colonies are a bright blue, pale yellow, or yellowish-green. Various colours occur side by side, and sometimes one portion of a colony will be blue and another yellowish-green."

Saville-Kent says of the colours of *Porites* on the Great Barrier Reef, "A light ochre, dark and golden or mustard yellow, and brown are the prevailing colours among the arborescent types. The surface of the corallum in the massive species, however, is often a delicate pink, a light or bright lilac, or (more rarely) pale yellow."

The genus *Goniopora* is closely related to *Porites* and also builds up great masses of spherical, lobate, encrusting coral. It appears to be more restricted in its recent geographical distribution than *Porites*, being confined to the tropical Indo-Pacific regions. The principal characters by which it can be distinguished from *Porites* is the presence of a secondary series of twelve septa, so that there are twenty-four septa in each calyx instead of only twelve.

The polyps are said to be very extensile and to possess usually twenty-four long digitate tentacles arranged in a single ring.

We have at present no knowledge of the number and arrangement of the mesenteries or other details of anatomical structure.

MONTIPORA.—The genus *Montipora* is another important reef-building coral, widely distributed in the tropical seas of

¹ J. F. Duerden, *Mem. Nat. Acad. Sci. Washington*, vol. viii., 1902, p. 550.

the Old World, but absent in the Atlantic Ocean and West Indian waters. Many specimens are of very great size, and almost every possible form of growth such as the branching, encrusting, massive, foliate, etc., may be represented. One particular form of this coral was called by Rumphius Elephant Ear and others Sea-rose or Sea-cauliflower. These varieties are described by Pallas under the name *Madrepora foliosa*.

There is no difficulty in determining at once, by the examination of a dried specimen with a hand lens, that all parts of the colony are profusely perforated.

The calices are small, rarely exceeding 1 mm. in diameter, and do not project above the general surface of the corallum. The genus can be distinguished from *Porites*, with which it is most likely to be confounded, by the presence of a considerable amount of coenosteum between the calices, perforated by numerous and relatively large pores.

The details of the calicular structure are more difficult to ascertain, not only on account of their small size, but because the septa are reduced by perforation to rows of minute spines or trabeculae of great variability. An examination of a large number of calices, however, leads to the conclusion that six primary septa are always represented and usually six secondary septa as well. In some specimens, but not in all, the two directive septa of the primary series are larger than the others and meet in the centre of the calyx.

According to Saville-Kent the colours of *Montipora* on the Barrier Reef are almost as brilliant and as varied as the colours of *Madrepora*.

ANACROPORA, a genus confined to Indo-Pacific seas, is in some respects intermediate between *Madrepora* and *Montipora*. It has a characteristic method of growth, thin branches diverging at wide angles which tend to form tangled masses of low growth.

The walls of the calices protrude from the surface, and there are definite septa and costae as in *Madrepora*, and the calices are separated by coenosteum as in *Montipora*.

TURBINARIA.—The genus *Turbinaria* is generally classified with the *Madreporidae*. It differs, however, from the other

members of this family in some important particulars, and it is possible that when we have a more extended knowledge of its anatomy it may have to be considered as the type genus of a separate family.

The name is derived from the shape assumed by the most common variety or species of the genus, which is that of a large shallow bowl attached by a thick stem to the rock. The genus is widely distributed in shallow water in the Indian and Pacific Oceans, but does not occur in the West Indian waters.

It seems to be a characteristic feature of the genus that



FIG. 40.—*Turbinaria*. A young stage in the development of a colony. Nat. size.

in the early stages of its growth it has a shape like a mushroom with a flat or slightly concave disc and a ring of calices round the margin (Fig. 40).¹ By marginal growth, these calices become situated on the upper side of the disc, and are succeeded by others that are formed on the growing edge. This process is continued until the bowl shape is attained (Fig. 41).

The other varieties of form assumed by the adult corallum seem to be due to irregularities in the growth of the margin, and thus great sheets of *Turbinaria* are formed with fringed or foliate edges, plates, or dishes which seem to have lost the original stalk and form encrusting laminae over the rock or over other laminae of the same coral. Colonies of this genus which ramify in the manner of the *Madrepore* and other corals, are not common, but do occasionally occur. The corals of this genus also reach great dimensions. A specimen in the British Museum of irregular shape with a boundary of 16 ft. 8 in. is 1500 lbs. in weight.²

The upper surface of the corallum is provided with a

¹ Pace, *J. Linn. Soc.* xxviii. p. 361.

² F. J. Bell, *J.R. Micr. Soc.*, 1895, p. 148.

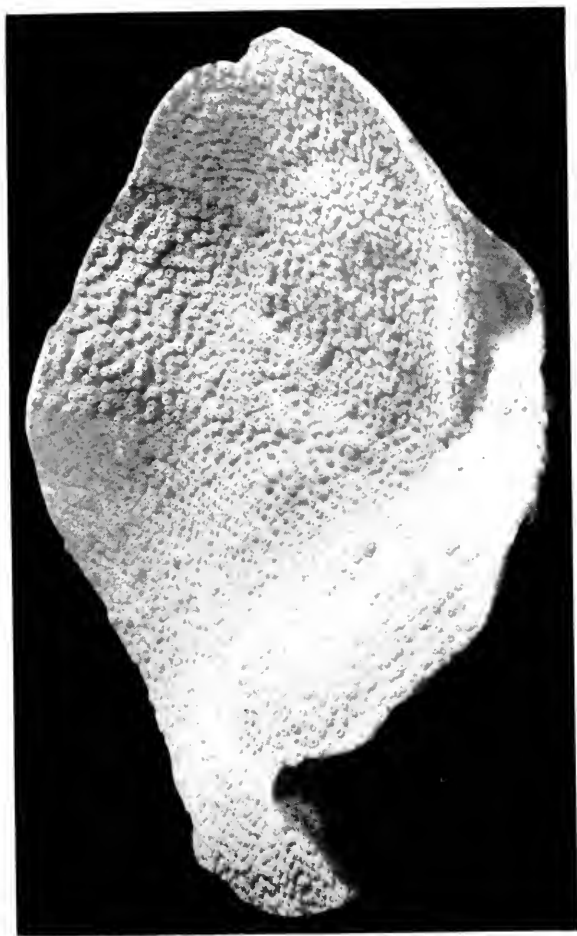


FIG. 41.—*Turbinaria*. Surface view of a large bowl-shaped colony. The stalk of attachment is hidden beneath the bowl. $\frac{1}{4}$ nat. size.

large number of calices, which usually project a little from the general surface, and between them there is a variable amount of profusely perforated coenosteum which is not marked with cestal ridges.

The surface of one of these large *Turbinarias* affords an interesting study in variation. The student finds on the same frond calices that vary in size from 0.5 mm. to 1.0 mm. ; he finds that some calices project from the surface with thick cup lips and others are almost flush with the surface, and that in some parts of the corallum the calices are crowded together and in others are separated by considerable areas of coenosteum.

A similar excessive variation is also seen in the details of structure of the calices. The number of septa rarely exceeds twenty-two, but any number from seventeen to twenty-two may be crowded in a full-grown calyx. The septa are usually of approximately equal size, so that it is impossible to recognise the directive septa or to distinguish the primaries from the secondaries. The most remarkable feature of the septal system, however, is that the number of septa does not seem to bear any relation to the number twelve, and it is this peculiarity which renders the position of the genus in the family *Madreporidae* a doubtful one. A columella is usually present, but it is also very variable. There are no pali.

The pairs of mesenteries of *Turbinaria* correspond in number with the septa. There are two pairs of directive mesenteries arranged in a plane almost parallel with a radius of the colony. The number of other pairs of mesenteries varies and is not the same on the two sides of the directive plane.

According to Saville-Kent "the tentacles are numerous and simply subulate," and the colour of some of the varieties is rose-pink or yellow.

It has been supposed that in an early stage of the development of a *Turbinaria* colony there is an important difference between this genus and *Madrepora*. It was suggested that whereas in *Madrepora* the primary polyp and the calyx it forms becomes the axial polyp on the sides of which the

young buds are formed, in *Turbinaria* the primary polyp is suppressed and becomes engulfed in the corallum at a stage such as that shown in Fig. 40. Pace has shown, however, that the primary calyx does persist, but instead of standing up straight from the base it bends to one side and therefore appears in that stage as one of the marginal calices.

Notwithstanding this peculiar character, and others which have been already mentioned, the general characters of the profusely perforated corallum and the structure of the calices do not justify the removal of the genus from the family Madreporidae in the present state of our knowledge, but our knowledge is still very imperfect, and a detailed study of the structure of the polyps and particularly of the method of gemmation might lead to results of importance which would definitely settle the position of the genus in our system.



FIG. 42.—*Pyrophyllia inflata*. Persian Gulf, 156 fathoms. 8 diams. From *Manchester Memoirs*, 54, 1910.

PYROPHYLLIA.¹—A genus of unknown affinities. A remarkable little solitary coral not more than 5 mm. in length by 1 mm. in diameter was found in a sample of the sea-bottom obtained by Mr. Townsend in the Persian Gulf at a depth of 156 fathoms (Fig. 42).

Its most characteristic feature is that it exhibits almost perfect octo-radial symmetry. There are eight large septa (the protosepta) and eight small ones (the metasepta), never more nor less (Fig. 43). In the centre of the calyx there is an undulating laminate columella. Externally, the thecal wall is marked by from fifteen to twenty annular ridges, which may be considered to indicate a series of intermittent stages of growth, and there are sixteen costal spines and crests on each annulus corresponding with the

¹ S. J. Hickson, *Proc. Zool. Soc.*, 1911, p. 1037.

septa. The shape of the coral is that of a slightly bent cone with an inflation at the apex. The apex of the cone is, of course, the base of the coral, and is the part which is formed first in development.

This inflated end of the *Pyrophyllia* is of some special interest, because it is obviously not adapted for attachment to a support—and indeed never shows any signs of attachment. This leads to the conclusion that the living *Pyrophyllia* is a free coral, but if it is free where does it live? It is inconceivable that it lives upright among the loose rubble of shells with which it was found. It must have come therefore with the currents from some other locality or have fallen from the surface waters.

Unfortunately we have no information concerning the habitat or anatomy of the polyp that forms this coral, and every one of the many hundreds of specimens that were obtained were more or less water-worn or broken. Until the living polyp is discovered we shall have no satisfactory answer to the many questions that arise concerning *Pyrophyllia*, but it is possible that the dilated base enclosed a bubble of gas which kept it suspended in the water, and that the habit of this coral is pelagic.

It is very difficult at present to determine the zoological position of this interesting genus.

The only recent coral that appears to be related to it is *Guynia annulata*¹ from 92 fathoms of water on the Adventure Bank, in the Mediterranean Sea, which Duncan considered to be related to a family of corals belonging to the extinct Order Rugosa. There are, however, some important differences between *Guynia* and *Pyrophyllia* which

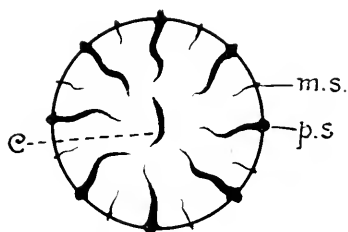


FIG. 43.—Diagram of the septa of *Pyrophyllia inflata*. *c.*, columella; *p.s.*, primary septa; *m.s.*, secondary septa. From *Manchester Memoirs*, 54, 1910.

¹ P. M. Duncan, "The Structure and Affinities of *Guynia annulata*," *Phil. Trans. Roy. Soc.*, 1872, p. 29.

render the relationship very obscure. *Gynia* has the same annular ridges of growth, and it has usually the same number of large and small septa, but it is attached by its side to shells and has no inflated base.

The only other coral with which it seems to have any true relation is the extinct genus *Conosmilia* from the Tertiary deposits of Australia.

CHAPTER V

ALCYONARIAN CORALS

"Qui navigavere in Indos Alexandri milites frondem marinarum arborum tradidere in aqua viridem fuisse, exemptam sole protinus in salem arescentem, iuncos quoque lapideos perquam similes veris per littora."—Pliny, *Nat. Hist.* xiii. cap. 51.

THE large group of marine organisms known as the Alcyonaria has received its ordinal name from a common spongy zoophyte called Alcyonium which is found in shallow water and sometimes above low-water mark on the British and other European coasts.

Lumps of dead Alcyonium, with their four or five lobate processes, which have been washed ashore, have a very rough resemblance to a human hand with swollen and distorted fingers, and on this account the British species was given by Ellis the name *Alcyonium manus marina*, and is known in popular works on natural history as "Dead Men's fingers."

But we are not concerned in this book with Alcyonium, for although it does secrete calcareous spicules to support its structure it is relatively soft or spongy in texture and could not be brought within the scope of any recognised definition of the word coral.

However, Alcyonium is closely related to many other marine zoophytes which do form a hard continuous skeletal structure which have been and still are called "corals"; in fact, the well-known precious coral of commerce, the first of all others in history to receive the name coral, is a member of the group. As the Alcyonaria form a very well-defined Order of the Animal Kingdom, notwithstanding

the great variety they exhibit in the form and texture of the skeletal structures they produce, it is necessary to relate in a few words some of the anatomical characters which distinguish them.

As with many other corals, the Alcyonaria are colonial in habit; a large number of animal organisms of the form known as Polyps, in organic connexion with one another by a system of nutritive canals, constitute the structure which is known as the Alcyonarian. In most of the Alcyonaria all the polyps of a colony have a similar anatomical structure, showing when fully expanded eight pinnate

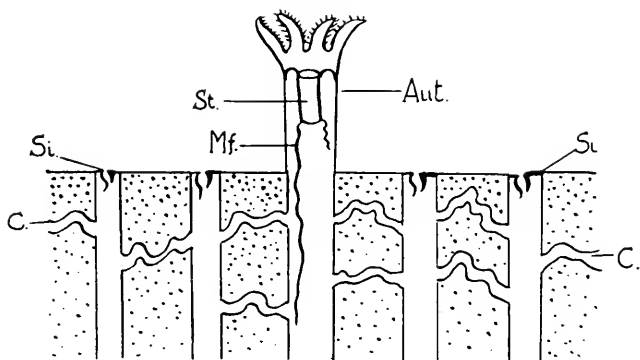


FIG. 44.—Diagram to illustrate the structure of a dimorphic Alcyonarian. *Aut.*, autozoid; *C.*, endodermal canals; *Mf.*, mesenteric filaments; *Si.*, siphonozooids; *St.*, stomodaeum.

tentacles (Fig. 47, A.) and a general octoradiate symmetry of their organs, but in some genera, which are usually more spongy in texture than the others, there are in addition to the normal polyps or autozooids a large number of polyps which are arrested in development and never produce any tentacles. The latter are called the siphonozooids, and their primary function appears to be to create and maintain by means of ciliary action a flow of water through the canal system (Fig. 44).

Another character of the Alcyonaria, with very few exceptions, is the power of forming calcareous spicules. These spicules, varying greatly in size, shape, and distribu-

tion in the colony, afford one of the principal characters for the recognition of genera and species (Fig. 45).

In many cases the spicules cease to grow when they have reached a certain size and remain free from one another in the soft tissues, so that when the colonies die and the soft tissues are dissipated the spicules are distributed. But in others (*e.g.* *Corallium* and *Tubipora*) the spicules grow until they come into contact with one another and become tightly packed together. In this way a skeletal structure persists after death which represents the general form of the colony.

The genus *Heliopora* stands by itself as the only recent Alcyonarian that forms a continuous calcareous skeleton without spicule formation after the manner of the *Madreporaria*.

In another group of Alcyonaria which may be called the Gorgonians, the substance Keratin, closely allied to horn, enters into the composition of the skeletal structures. In *Gorgonia* itself, an axis is

formed of pure keratin, and this supports a thin crust or bark consisting of the polyps, with their connecting tissues and the calcareous spicules. On the death of the colony the bark is dissolved and washed away by the sea, the horny axis alone remaining intact.

In some Gorgonians the horny axis is impregnated with calcium carbonate, and in others the axis consists of alternate horny nodes and calcareous internodes.

There are a few Gorgonians which consist of a long unbranched stem attached by a disc-shaped expansion at the base to a foreign substance, but usually the main stem divides into secondary branches, and these ramify again and again before they terminate in numerous delicate free

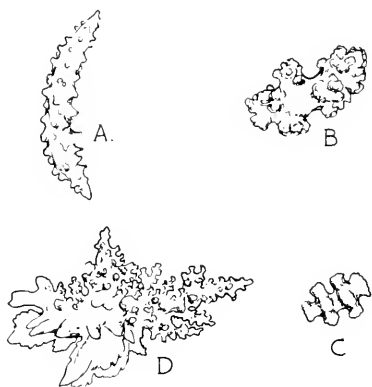


FIG. 45.—Spicules of Alcyonaria. A, *Melitodes*; B, *Isis*; C, *Gorgonia*; D, *Echinomuricea*.

twigs. In some forms the branching takes place in all directions, forming bushy or tree-like structures, but more commonly the branching is in one plane only, so that the structure is fan-shaped or flabelliform.

The presence of the horny substance in the axis of the Gorgonians is of advantage to them in many sea localities where the tides and currents are particularly strong, in that it gives them the power to bend without breaking, the calcareous skeleton of the purely calcareous Alcyonaria being quite inflexible. In the tropical seas it is a wonderful sight to see through a few feet of the clear water the great tufts of brightly coloured Gorgonians attached to the piles of a pier, or in favourable situations on the reef waving backwards and forwards with the rise and fall of the water. An intelligent observer seeing them for the first time would probably be inclined to classify them with the other corals of the neighbourhood, but would notice that they differ from them in their flexibility.

The Gorgonians, however, are not the only coral-like organisms that are flexible, and the famous work by Lamouroux published in 1816, entitled *Polypiers coralligènes flexibles*, included Algae, Polyzoa, Hydrozoa, as well as some of the Anthozoan corals. Nevertheless the popular expression "flexible corals" has become more restricted, and is still sometimes used to signify only the Alcyonarian corals with a horny flexible axis.

In the course of the descriptions that are given of different kinds of Alcyonarian corals reference will be made to their colours. These colours are, as a rule, due to a pigment in the calcareous spicules which is permanent, that is to say, it does not fade or disappear when the coral is dried. The permanence of these colours is really remarkable, as is exemplified by the colour of the red coral beads in the ancient British shield found in Lincolnshire (see p. 241), which is probably as bright now as it was several hundreds of years before the Christian era, when the coral was dredged up from the sea. The Alcyonarian polyps when fully expanded in the seas are usually either transparently white or of a faint pale pink colour, and when they are retracted

the corals have very much the same general colour in the sea as they have when dried and stored in a museum.

There are, however, some exceptions to these general rules (see *Primnoa*, p. 129, *Tubipora*, p. 112).

In the *Madreporaria*, on the other hand, the colours are almost invariably due to a pigment diffused through the soft tissues which is soluble in alcohol and fades away soon after the death of the corals. Dried and preserved *Madreporarian* corals, therefore, never show the nature of the brilliant colours they may exhibit when they are alive.

It is interesting in this connexion to notice the difference there is between the exhibits in the cases of a museum of the *Alcyonarian* and *Madreporarian* corals. On the one hand, we have an endless variety of bright colours and on the other a monotonous dull stony white.

CORALLIUM.¹—The first coral mentioned in literature and the most famous throughout the ages for its beauty and for the occult powers it was supposed to possess, is the red or precious coral of the Mediterranean Sea. In another chapter will be given a short account of the history of the trade in this substance and of the myths concerning its origin and properties. Here we are only concerned with the study of the red coral from the zoological point of view.

The hard red coral substance that is sold in the shops is the axis or central supporting core of a dimorphic colony of *Alcyonarian* polyps. When the coral is alive, this axis is covered by a soft bark or crust, through which penetrates an elaborate system of canals, which bring the two kinds of polyps, the *Autozooids* and *Siphonozooids*, into communication with one another (Fig. 46).

When a colony of *Corallium* that has been just removed from the sea is placed in a glass vessel and allowed to remain there for a little while, the white and almost transparent *autozooids* gradually expand and project from the surface of the bark, producing an effect which the earlier naturalists mistook for the flowers of a plant (Fig. 47). Each *autozooid* bears a crown of eight pinnate tentacles, formerly regarded

¹ See the beautifully illustrated memoir by H. de Lacaze-Duthiers, *Histoire naturelle du Corail*, Paris, 1864.

as the petals of the flower, and through the transparent cylindrical body wall may be seen thread-like structures, which on further microscopical examination prove to be the throat (stomodaeum), the eight mesenteries, and the eight mesenteric filaments of a typical Alcyonarian polyp.

In the months of May and June the autozooids contain a number of spherical or oval bodies, and occasionally one of them will squeeze through the mouth and swim away.

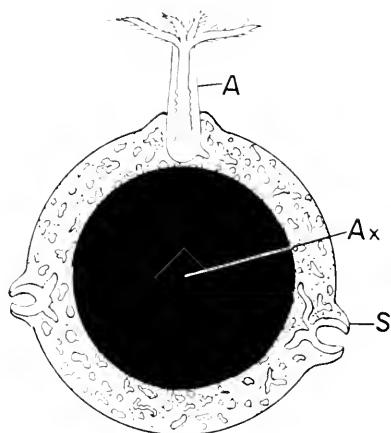


FIG. 46.—A diagram to show the structure of a branch of *Corallium* as seen in transverse section. In the centre is the axis (Ax.) and covering this is the coenenchym, a soft fleshy substance containing the endoderm canals and spicules and bearing the autozooids (A.) and the siphonozooids (S.). \times 4 diams.

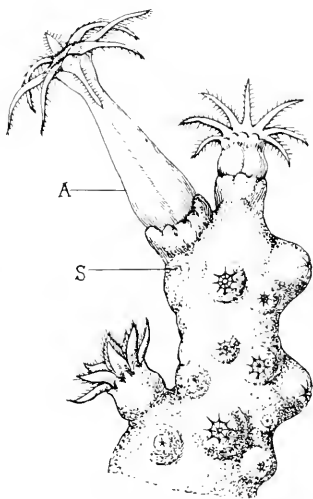


FIG. 47.—*Corallium nobile*. Mediterranean Sea. A., an expanded autozooid. S., a siphonozooid. From a drawing by H. de Lacaze-Duthiers. \times about 8 diams.

These are the larvae, for *Corallium* presents us with one of the rare examples of the occurrence of viviparity in the group of the Alcyonaria. *Corallium nobile* of the Mediterranean is also rather exceptional among corals in being hermaphrodite. Some branches of a single specimen may be male and others female, or a single branch may support both male and female polyps.

When all the autozooids are fully expanded, the outstretched tentacles form an almost complete gauzy veil over the surface of the branch, so that no minute organism that

swims within a polyp's length of the coral can possibly escape the batteries of nematocysts with which the tentacles are armed.

Between the autozooids a number of small yellowish-white spots can be seen, each of which is provided with a little mouth when the coral is alive and expanded. Until recently these spots were thought to be young polyps which develop into autozooids, but it was shown by Moseley that they are a different kind of polyp, and perform a different function from the polyps which expand (Figs. 46 and 47, S.).

They are called the siphonozooids. They have no tentacles and the mesenteries are very much reduced, but

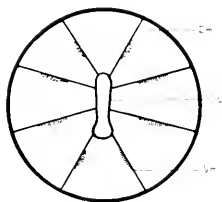


FIG. 48.—Diagram of a transverse section through an Alcyonarian polyp. *St.*, stomodaeum; *Dm.*, dorsal mesenteries; *Vm.*, ventral mesenteries.

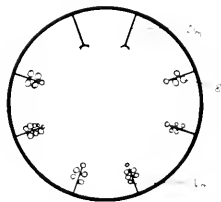


FIG. 49.—The same, taken at a lower level than the stomodaeum. *g.*, the gonads situated on the lateral ventral mesenteries.

the stomodaeum is provided with a broad groove armed with very powerful cilia, by means of which the currents of water in the canal system are maintained.

The bark or coenenchym of *Corallium* is of a dark-red colour, due to the presence of a large number of red spicules of calcium carbonate about $\cdot 07$ mm. in length (Fig. 50). The spicules are formed by certain specialised cells in the ectoderm covering the bark. These cells become detached from the rest of the ectoderm and sink down into the substance of the bark, where the spicules continue to grow, until they become jammed together to form a solid mass of coral. In this way the axis is formed and grows. The increase in diameter of the axis of the stem and branches does not seem to take place by the addition of newly formed layers of jammed spicules, but continuously, so that in a

section of the coral growth rings are either absent or only faintly indicated.

It is this continuity of the growth, together with the completeness with which the spicules are jammed together so as to leave no space between them, which gives to the red coral its hardness, purity, and lustre when polished. There are many other Alcyonaria in which the spicules become pressed together in this way, but no others in which the amalgamation is so complete that their individual outlines and all intervening crevices and spaces between them are entirely lost. It is difficult to give a general description of the shape of the spicules in a few words, as they vary

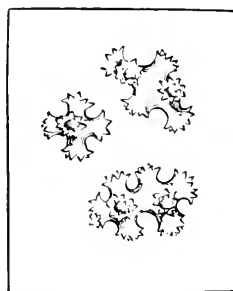


FIG. 50.—Spicules of *Corallium nobile*. 200 diams.

enormously according to their age and position. In the younger stages they are usually oval or spindle-shaped, with swollen, spiny extremities, and bearing two circlets of four large spiny tubercles on the body; but as they increase in size they seem to develop in a great variety of ways. The spicules of some other species of *Corallium* can be distinguished from those of the Mediterranean *Corallium nobile* by their peculiar "opera-glass" shape, a modification of the type produced by an uneven development of the two circles of tubercles; but the spicules of all the species are so variable that they never afford a very reliable character for the systematic arrangement of the genus into species.

The red coral of the Mediterranean Sea constitutes the species *Corallium nobile* (Pallas) or *C. rubrum*, Lam. Of these two names the former has undoubtedly the right of priority.

The same species extends into the Atlantic Ocean, and a fishery of red coral on a smaller scale has been established in the Cape Verde Islands and Madeira.

Other species of the same genus have been found off the coasts of Japan, Timor, Djilolo, and Mauritius, and a few specimens in deep water off the west coast of Ireland, in the Bay of Biscay, and other localities.

Until comparatively recent times there was a considerable trade in red coral imported into Japan from Italy, because the Daimyo of Tosa had prohibited the collection and sale of the coral that was occasionally captured by the fishermen in the Bay of Tosa; but after the Meiji reform of 1868 a very active industry sprang up, coral was found in other localities than Tosa, where it was first discovered, and gradually the exports of coral caught up and passed the imports. In 1901, coral to the value of £50,000 was exported, and most of this was sent to Italy, where the fishery was showing signs of exhaustion.

The colour of these corals varies from white,¹ through various shades of pink to red, and in some of the Japanese varieties there is a yellowish tinge. The colour seems to be very variable in all the shallow-water species. The deep-sea forms from the Atlantic Ocean are usually white, but the specimens of a species of *Corallium* obtained by the Siboga Expedition, at a depth of 1089 metres, off Djilolo, was of a full red colour. The variety called black coral, not to be confounded with the "black" coral which is described on pp. 244-250, is supposed to be due to some post-mortem change in the organic constituent of the coral; but a black specimen obtained in the great depth of 1525 fathoms in the Atlantic Ocean by the *Challenger* Expedition owed its colour to a deposit of peroxide of manganese.

The attempt to group the specimens of this genus into satisfactory specific groups is beset with difficulties. Both colour and form seem to be so variable that they cannot be relied upon as specific characters, and such differences as are observed in the shape of the spicules and the degree of retraction of the autozooids are difficult to express in precise terms. So far as can be judged at present, however, the Mediterranean red coral seems to be a distinct species. It differs from all the other forms that have been examined in two interesting peculiarities, (1) that the autozooids bear the eggs and sperms and not the siphonozooids, and (2) that it is

¹ White coral, although not so valuable as the red and pink varieties, is now largely used in jewellery. It is cut from the stems of white species of the genus *Corallium*, and is principally imported from Japan.

viviparous. It is possible also that it differs from the other species in being sometimes hermaphrodite.

These are points, however, which are still in need of further careful investigation.

TUBIPORA.—An Alcyonarian coral that has a very wide geographical distribution in shallow tropical sea-water is the well-known Organ-pipe coral (*Tubipora musica*). The popular name was first given to it by Tournefort in 1719, and has reference to its construction by a number of cylindrical tubes arranged almost parallel with one another, and bound together by a series of transverse plates or platforms, so that, viewed in section, there is some resemblance to the arrangement of the pipes of a great organ (Fig. 51).

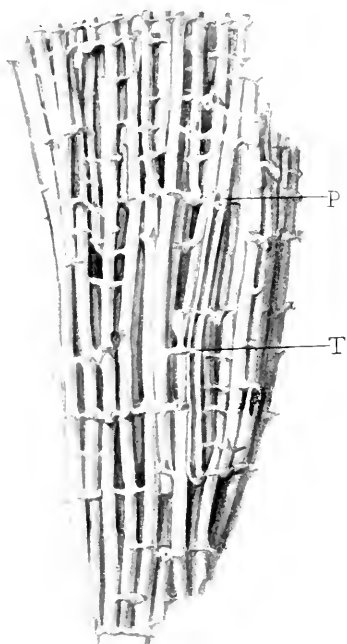


FIG. 51.—*Tubipora musica*. A piece of a large colony, showing the tubes and the horizontal platforms from which young tubes spring, P. One of the tubes, T., has been dissected to show the tabulae. Nat. size.

It is found alive, attached to shells, corals, or stones, on the reefs of many of the shores of the Red Sea, Indian Ocean, the tropical Pacific Ocean, and the West Indies; and the dead corals are cast up on to the beaches of some of these shores in countless

numbers. When seen alive in a calm rock-pool, the familiar form of the coral is hidden by a mantle of emerald-green tentacles, but as the tide falls and the polyps contract, the green colour fades away, exposing the ends of the red tubes of which the skeleton structures are composed.

The Organ-pipe coral arises from a flat membranous plate, which spreads over the surface of the substance to which it is attached. From this plate of attachment or

"stolon," as it is called, a number of tubes arise, which are bound together by a horizontal platform at a distance of a few millimetres from the base. Every tube passes through the platform, and at a distance of another few millimetres passes with its fellows through a second platform, and so on, through several platforms, until the surface is reached.

If two or three of these primary tubes springing from the base are traced through their whole length, it is found that they are not quite parallel, but spread out fan-wise in all directions, and from each of the platforms secondary tubes arise which fill up the spaces between the primary tubes, and thus in each series the number of tubes increases. By this manner of growth great dome-shaped masses of coral are formed which may reach the size of a man's head, but the time comes when the weight of the mass is too great for the support given by the few primary tubes that have sprung from the stolon, and then it is broken off by wave action, is rolled by the breakers, and eventually cast up on the beach.

On making an anatomical examination of a preserved specimen, it is found that the soft lining tissues of the polyps do not extend below the level of the second platform from the surface. The inner parts of the mass, therefore, are nothing but a skeletal structure for the support of the living surface; but the shelter they afford attracts many interesting examples of the aquatic fauna and flora, such as worms, mollusca, crabs, and other crustacea, encrusting sponges, polyzoa and algae, so that it becomes a miniature museum of strange creatures. Some of these organisms assist in the destruction of the inner tubes, and thereby hasten the time when the coral meets its fate by becoming detached from its base.

The polyps are all of one kind, and have the typical Alcyonarian structure. The mouth, at the distal extremity, is surrounded by eight pinnate tentacles, and the short throat or stomodaeum into which the mouth opens is connected with the body wall by eight mesenteries.

When the polyp is fully extended the body wall is continuous with the extremity of one of the red tubes. In

contraction the tentacles are first folded inwards over the mouth, and then the whole crown of tentacles, mouth, and stomodaeum are drawn downwards into the tube, and this is followed by the infolding of the body wall from above until the limit of the red tube is reached. When the contraction is complete the mouth of the tube is stoppered by the contracted polyp, and thus the exit of the water from the body cavity is prevented and the coral is able to retain its vitality, even if the coral, by the fall of the tide, is left for a few hours exposed to the tropical sun. The tubes are built up by the growth and fusion of a large number of spicules of calcium carbonate in the substance of the body wall. In the upper part of the contractile part of the body wall the spicules are small and scattered, in the lower part they are much larger, and in the region of the junction of hard and soft parts they have become so large that they are articulated together to form a firm skeletal wall.

The firm coral substance or "corallum" of *Tubipora* is constructed, therefore, in the same way as it is in *Corallium*, by the fusion or, to be more correct, the jamming together of Alcyonarian spicules. But whereas in *Corallium* the substance thus formed is quite compact, in *Tubipora* a number of spaces or pores are always left in the substance, by which the living tissues can maintain a connexion between the endoderm lining the inside of the tube and the ectoderm covering the outside. The Organ-pipe coral is therefore a perforate coral, and, like all perforate corals, its substance is brittle, and is rapidly broken up and disintegrated when exposed for any length of time to the action of the surf. It is also a tabulate coral, but the tabulae are very variable in form and frequently so different in character from the tabulae of *Millepora*, *Heliopora*, and many other corals that the name "tabula" does not seem to be strictly applicable.

In some tubes there may be found a flat plate of coral substance, dividing the cavity of the tube transversely on the level of a platform. Such a plate is obviously a tabula of the ordinary type. In other places the tabula is cup-shaped, and more frequently it is drawn out into a fine point

in the direction of the platform next below it, and then it may be called a funnel-shaped or "infundibuliform" tabula.

In many tubes, however, it is found that an infundibuliform tabula, instead of ending blindly, expands again to form an inverted funnel, the mouth of which is on a level with the next platform. Thus we find within the tube an inner tube, which contracts to a capillary size in the middle, a structure which is obviously of the same nature, but utterly unlike what is usually called a tabula in works on corals. The interpretation of these different forms of tabulae in *Tubipora* has been given elsewhere;¹ but it is important to note that the character of the tabulae varies enormously, not only in the tubes of a single specimen, but also in the different regions of a single tube, and it is therefore quite useless as a character for specific distinctions.

The genus *Tubipora* is one of the many genera of corals in which the question of species is one of extraordinary difficulty.

The lumps of this coral that are to be seen in museums in this country differ from one another in shape, in the size of the tubes, in the distance separating the platforms, and to some extent in the shade of red colour of the coral substance. All these characters, however, are so variable, so dependent upon the characters of the environment in which the corals grow, that any system of species founded upon them would fail on account of an indefinite number of intermediate varieties. On the shore of the Island of Celebes the author took the opportunity to collect and examine many hundreds of specimens that had been washed up by the sea and many scores of specimens alive on the coral reefs, and came to the conclusion that almost every variety that is known could be found on that one shore, and that there is complete continuity between one extreme variety and another. This does not entirely dispose of the question of specific grouping, as other characters may yet be discovered which do not exhibit the same degree of individual variability, but it

¹ S. J. Hickson, *Quart. Journ. Micr. Sci.* xxiii., 1883. These curious infundibuliform tabulae appear to have been first noticed by Ellis and Solander, *Zoophytes*, Plate 27, 1786.

leaves it in the position that at present only one species, of almost world-wide distribution in shallow tropical waters, can be recognised, and that species is *Tubipora musica* Linnaeus, formerly called *Tubipora purpurea* by Pallas and Tournef.

The Organ-pipe coral was used in very early times in Egypt to make into little beads for ornament, but seems to have fallen into disuse in all but the earliest dynasties. Rumphius has some interesting notes on the magical properties attributed to it by the Malays of his time. It was called the Batu swangi or Magicians' Stone, and was hung on the trees to prevent thieves from stealing the fruit, for any thief who stole fruit from a tree that it protected became affected with a rash of red pimples. It was also used in the form of a powder as a medicine to cure strangury.

TELESTO RUBRA.—A brief note may be added here on a rare little coral of which only a few fragments have been found in 20-40 fathoms of water off the islands of the Indian Ocean. The colony consists of a single upright tube, representing the body wall of a long axial polyp, which bears a few lateral branches of the same nature. The main stem and the long tubes which spring from it bear a number of prominent verrucae representing an equal number of lateral or secondary polyps.

In the method of colony formation this species agrees with the other species of the genus *Telesto*, but it differs from all the others in the fact that the spicules coalesce as they do in the genus *Tubipora* to form a compact but profusely perforated calcareous tube of a pink or pale red colour.

Small dried specimens of *Telesto rubra* might possibly be mistaken for isolated tubes of *Tubipora*, although they differ from that genus in the absence of anything corresponding with the horizontal platforms and in the way in which the young polyps are situated on the body wall of the old one. Moreover, in *T. rubra* there are eight shallow longitudinal ridges on the outside of the tubes, whereas in *Tubipora* the tubes are always perfectly smooth.

The largest specimens that have been found are only

70 mm. in height, and the tubes have a diameter of 2-3 mm.

The only known localities are Maldive Islands, 23-35 fathoms; Trincomalee, Rutland Island, 35 fathoms; and Andaman Islands in 45 fathoms.

PARAGORGIA.—In the deep waters of the Norwegian fjords there is found a large red branching Alcyonarian, which might be mistaken at first sight for a coarse overgrown precious coral; but an examination of one of the broken branches shows that it differs from *Corallium* in having no hard and imperforate axis, the substance of the branch right down to the centre being perforated by numerous canals.

This is the *Paragorgia arborea* or "Sea-cork tree" of the older writers, and it probably received its specific name because in magnitude it is better compared with a tree than with any other kind of vegetable growth.

It is impossible to say to what size it may attain in these great depths of water, far beyond the range of our vision, as it is so brittle that with the best methods at our disposal great difficulty has been found in bringing safely to the surface complete specimens. But from rough calculations based on a circumference of five or six inches of some of the large stems or branches that have been obtained it is probably no exaggeration to say that the height from the ground of some specimens must be over six feet.

In general anatomy the *Paragorgia* has many features in common with *Corallium*, but it is much more vascular, and the spicules never become so firmly interlocked and fused together as to form a hard stony skeletal structure.

The substance of a dried specimen is light and porous, and unless it is carefully handled is liable to break up into fragments.

The species has a remarkable distribution. It is common in the Norwegian fjords and extends North to the seas off Nova Zembla and Franz Josef Land. It has not been found in the British area nor off the Faröes and Iceland, but turns up again in cold deep waters off the western side of the North Atlantic. The most interesting feature of its

distribution, however, is that the same species occurs in deep water in the fjords of British Columbia and a closely allied species off the coast of Japan.

So far as our knowledge of its distribution goes, therefore, it seems to be a species confined to the cold deep waters of the Northern Hemispheres with two remarkable breaks in its continuity, one in the North Atlantic and the other the American continent. It affords, therefore, an interesting problem for students of geographical distribution.

HELIOPORA.—It was formerly supposed that *Heliopora* was a Zoantharian coral until Moseley, during the voyage of the *Challenger* Expedition, examined the polyps of some specimens at Samboangan and proved that they have all the essential characters of the Alcyonaria. But although it is an Alcyonarian it occupies a unique and isolated position in that Order on account of its massive corallum of crystalline calcium carbonate, by the absence of the characteristic Alcyonarian spicules, and by other structural peculiarities.

There is one character which distinguishes the corallum of *Heliopora* from all others, and that is the blue colour which gives it its specific name. There is no other coral belonging to any group that possesses this colour, and in every specimen of *Heliopora* that has been examined the colour either permeates the whole corallum or can be seen just below the surface in a fractured branch. On this account it has received the popular name of "The Blue coral."

The form of the colony is very variable. It may be branched like a stag's horn Madrepore, laminate, or almost massive, but the ends of the branches are usually blunt and lobed. It sometimes reaches a size of three or four feet in diameter by two feet or more in height.

The surface of the corallum is rough and is perforated by two kinds of pores, which may be called the large pores and the small pores respectively, the small pores being very much more numerous than the large ones. On looking down into a large pore with a magnifying glass, a variable number of shallow ridges may be seen projecting into the lumen, which have a certain resemblance to the septa of

the Madreporarian corals, and are usually called the pseudo-septa (Fig. 52).

On making a section of a branch the pores can be seen to pass down into a series of parallel tubes with imperforate walls, which are divided into chambers by numerous tabulae (Fig. 53).

The corallum of *Heliopora* is therefore imperforate, tabulate, and dimorphic.

The structure of the soft parts of *Heliopora* is very peculiar. It might have been expected from the characters of the corallum that the polyps would prove to be dimorphic, and that we should find in the large pores autozooids and in the small pores siphonozooids. But this is not the case. In the large pores there are autozooids having the general characters of typical Alcyonarian polyps, but in the smaller pores there are only tubular diverticula of the canal system crowded with zooxanthellae and showing no trace of polyp structures. It has been suggested that these tubular cavities represent the body cavities of siphonozooids which have been lost by degeneration; but there is no evidence to support that view.

When the *Heliopora* is seen alive on the reef, the polyps are usually tightly retracted into the larger pores, but projecting from the grey surface a number of small thread-like worms display their active contortionate movements. These worms, belonging to the Polychaet genus *Leucodora*, are very frequently associated with *Heliopora*, and the thin

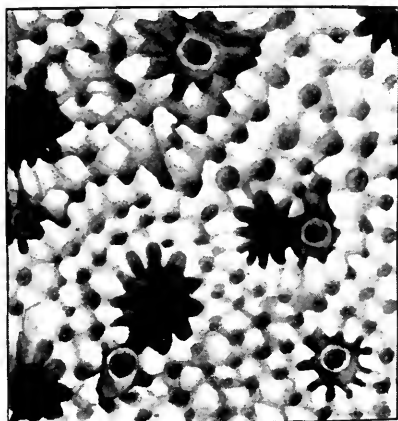


FIG. 52.—*Heliopora coerulea*. A part of the corallum highly magnified showing the large pores with their false septa and the small pores. Penetrating the surface are seen five smooth cylindrical tubes of the worm *Leucodora*.

calcareous tubes which they secrete may perforate the corallum in all directions (see Figs. 51 and 52), and are so numerous that they might be mistaken for a character of the coral. Specimens of *Heliopora* from the Maldive Archipelago are said to be free from this worm associate.

There is no record at present of the colour and appearance of the expanded polyps of *Heliopora*, and observations that have been made at low tide in the day time suggest that they are never expanded in such conditions. It is probable that like many other polyps they only expand at night.

Heliopora is a curiously isolated genus in the system of the Alcyonaria. It is the only recent genus of the Order Coenothecalia to which it belongs. It has no near relations among the Alcyonaria of the present day, but if we judge from the character of its skeletal structures, it may be closely related to a number of corals (*e.g.* *Heliolites*, *Polytremacis*, etc.) which, in the early history of the world, flourished on the reefs, but have long since become extinct.

Heliopora itself can be traced back through the Eocene to the Cretaceous period, but *Heliolites* and many allied genera died out before the close of the Palaeozoic period, and *Polytremacis* and others survived only to early Tertiary times. *Heliopora* is therefore the only survivor of a long line of ancestors with a pedigree extending back to the earliest times of which we have any record of corals, and so far as we can judge from its abundance on some reefs and the massive size it attains shows no signs of following its ancestors to extinction.

The survival of *Heliopora* is a matter of special interest, because most of the common corals of modern reefs, such as *Tubipora*, *Millepora*, *Madrepora*, and *Porites*, are of comparatively recent origin.

ISIS.—The coral that was called by the older writers the King Coral is the first of the few examples we shall consider in this chapter of the *Polypiers coralligènes flexibles* of Lamouroux. In general structure it presents similar features to those of *Corallium*. There is a hard axis covered by a thick coenenchym bearing the polyps, but in *Isis* the polyps

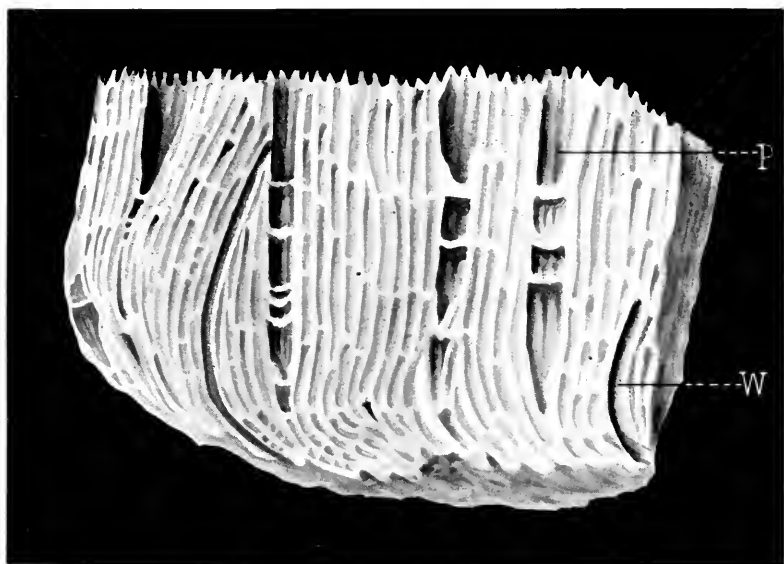


FIG. 53.—*Heliopora coerulea*. A vertical section of a part of the corallum showing the large pores P with their tabulae and numerous smaller pores between them. At W the corallum is pierced by a worm tube. $\times 10$ diams.

are all of one kind, similar to the autozooids of *Corallium*, and the axis consists of alternate horny nodes and calcareous internodes (Fig. 54).

This constitution of the axis renders the coral and its branches capable of bending in any direction without breaking, and is in striking contrast to the axis of *Corallium*, which is perfectly rigid and can only resist the force of the sea tides by virtue of its solidity and strength.

There is a passage in the book on Zoophytes by Ellis¹ which is worth quoting here as it expresses remarkably well the meaning of this structure of the axis of *Isis*. "These joints are an admirable contrivance of Nature to secure the little branches of these animals from being torn to pieces. Without this they could not arrive to the height of which some of them are found, viz., of two or three feet, for by bending freely to and fro with these soft joints they easily resist the violent motions of the sea."

The colony of an *Isis* is usually branched in one plane forming a fan-shaped coral, but specimens are sometimes found in which the ramification is less regular and an aggregated mass of irregular branches is the result. The terminal branches are thick and end bluntly.

The calcareous internodes of the main stem may be as much as 10 mm. in length and 10 mm. in diameter and delicately fluted with grooves in which the nutritive canals of the coenenchym lie. The horny nodes, which shrink and become brittle when dry, are about 3-4 mm. in thickness.

Among the many genera which are included in the family



FIG. 54.—*Isis hippuris*. The axis of one of the terminal branches of a large colony showing the horny nodes and calcareous internodes. Nat. size.

¹ *The Natural History of Zoophytes*, by John Ellis, 1786, p. 105.

Isidae, to which *Isis* belongs, there are various modes of ramification, and it is important to note, therefore, that *Isis* is one of those in which the branches always arise from the calcareous internodes. The species with which we are most familiar is called *Isis hippuris*. It is found in many shallow-water localities in the W. Indies and in the Pacific



FIG. 55.—*Isidella neapolitana*. Nat. size.

and Indian Oceans. It was well known to Rumphius,¹ who says that it was valued by the natives of Amboyna and the neighbouring islands as an antidote against dysentery, cholera, and other diseases. Pallas states on the authority of Imperato that *Isis hippuris* occurs in the Mediterranean Sea, but there appears to be no recent record of its occurrence either north or south of tropical waters.²

ISIDELLA. — Belonging to the same family as *Isis*, a much more delicate coral called *Isidella* is found in the Mediterranean Sea, in

deep water in the fjords of Norway, and in the Bay of Biscay.

In this form the ramification is more diffuse and usually dichotomous, and the branches arise from the horny nodes and not from the calcareous internodes as they do in *Isis*. The internodes are long, slender, and smooth; the nodes are

¹ The *Accarbaar puti* of the Malays (see p. 247).

² For a further account of this species see J. J. Simpson, *Journ. Linn. Society*, xxxvii., 1906.

very short. The coenenchym covering the branches is very thin (Fig. 55).

There is a passage in Pliny's *Natural History*, viii. cap. 52, which has given rise to some controversy. It may be translated, "Juba states that about the islands of the Troglydtes there is a shrub found out at sea called the 'Hair of Isis.'" It is very unlikely that such a name would have been given to the coral now called *Isis hippuris*; but it may have been given to the beautiful and delicate *Isidella* from the Mediterranean Sea in the first instance, and the same name given at a later period to *Isis hippuris* on account of its similarly jointed axis.

MELITODES.—In many regions of the tropical seas there may be found some very brightly coloured flexible corals which might, at first sight, be attributed to the family Isidae, as they also exhibit a "contrivance" of alternate nodes and internodes in the axis. Many of these belong to the genus *Melitodes*. A critical examination of the axis shows that it is quite differently constructed from the axis of *Isis*, for, instead of being solid, both nodes and internodes are perforated by canals, and for this reason the genus and its allies are placed in a separate family—the Melitodidae. The largest and probably the commonest of these is the species *Melitodes ochracea*, known to the older writers as the Red King Coral.

The colour is very variable, as it is in all the species of the genus, and may be either uniformly dark red or dark

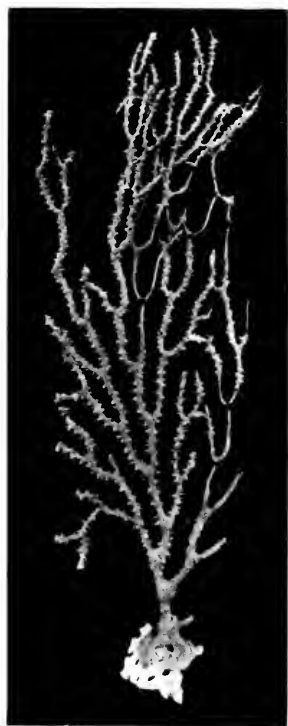


FIG. 56.—*Wrightella robusta* from Singapore. The genus *Wrightella* is closely related to *Melitodes*. Nat. size. After Shann, *Proc. Zool. Soc.*, 1912. Pl. LXII.

red and chrome yellow, the two colours being variously disposed.

When dried the coral is very brittle, so that it is difficult to obtain a perfect specimen for a museum, but it is known that the species may attain to a height of 3 feet and have a main stem half an inch or more in diameter.

On the reefs and in shallow water of the Indian Ocean a dwarf species, *Melitodes variabilis*, is found which exhibits very remarkable variation in the colour schemes. For example, on one reef in an atoll of the Maldivé Archipelago the nodes were all red, but the internodes were grey or red or pale yellow or salmon coloured. From other localities in the same archipelago specimens were found with yellow nodes and red internodes, with grey nodes and grey internodes, with red nodes and orange internodes, and many other variations.

The Alcyonarian flexible corals with an unjointed axis present such a great variety of form and minute structure that they are now divided up by the systematists into a very large number of genera and species. To attempt to describe the characters by which even the genera are distinguished from one another so as to give the reader a guide to the determination of the generic names would be a task that would take far more space than can be allotted to this group of corals. A few well-known genera have been selected, therefore, which will illustrate some of the more important characters of the families they represent.

The word *Gorgonia* as applied to flexible corals of some kinds is of very ancient origin and may have been derived from the Gorgones, the mythical ladies whose hair was said to be entwined with serpents ; but it is quite impossible to determine whether the classical writers applied the name to any one kind of flexible coral or to any kind of marine product having a black horny axis. The same sort of errors and myths gathered round the Gorgonians as round the red coral, and it is evident that they were regarded as of the same nature as *Corallium*.

Pliny¹ says "*Gorgonia nihil aliud est quam curalium* ;

¹ xxxvii. 10. 164.

nominis causa, quod in duritiam lapidis mutatur emollitum in mari; hanc fascinationibus resistere adfirmant."

Such a definition of a coral which asserts that it is soft in the water and turns hard on exposure to the air, and that it has the power of resisting fascinations, may not be satisfactory to the modern zoologist, but it, at least, lends support to the view that the Romans regarded the Gorgonians as something of the same nature as corals.

At the present day the generic name *Gorgonia* is very much more restricted than it was even at the beginning of the last century, and a host of new generic names have been invented for many of the Gorgonians of the old writers. These genera are divided into six families, of which four—the Gorgoniidae, Gorgonellidae, Plexauridae, and Primnoidae—are usually represented in museums by typical specimens.

There are three principal characters distinguishing the Gorgoniidae from the other five families. The axis is horny without any admixture of calcareous matter, the coenenchym is thin, and the polyps are retractile.

The axis is variously but usually profusely and delicately ramified, and in dried and retracted specimens the position of the zooids is represented by more or less prominent mounds or verrucae on the coenenchym.

GORGONIA.—One of the most familiar of the Gorgoniidae is the *Gorgonia flabellum*¹ of the shallow waters of the West Indies and other localities of the tropical Atlantic, which forms delicate fan-shaped structures by the profuse anastomosing of slender branches arranged in one plane.

Other genera of Gorgoniidae, such as *Leptogorgia* and *Pterogorgia*, form immense tufts or shrubs ending in long delicate branches which bend in all directions with the movements of the water, like grass in the wind, and with their brilliant purple, yellow, and red colours contribute to the brilliancy of the pools of the coral reefs in which they are often found. These beautiful and variously coloured corals form an effective display in a museum case.

In some respects, however, the most interesting member

¹ *Rhipidogorgia*.

of the family is *Gorgonia verrucosa*, the only representative of its kind in the British area, and being common in the Mediterranean Sea was probably one of the first of the Order to be given the name Gorgonia. Unfortunately systematic controversy has raged round this common species, and it has been shifted about from one genus to another and from one family to another according to the weight attached to particular characters by different writers.

The view that will be accepted in this book is that its proper generic name is Gorgonia and that its proper family is the Gorgoniidae, but it should be stated that some authorities consider that it should be called Eunicella and given a place in the family Plexauridae.¹

The controversy in this case really turns on the question whether the coenenchym should be described as thick or thin. It is, as a matter of fact, thicker than it usually is in the Gorgoniidae and thinner than it usually is in the Plexauridae, and the species in this respect as in others is intermediate in character between the families, but it may be held that being in such a doubtful position it should be classed with the Gorgoniidae on historical grounds.

Gorgonia verrucosa, sometimes called the Sea-fan (Fig. 57), is found in shallow water in the Mediterranean Sea and on the coasts of Brittany, Devonshire, and Cornwall. It grows to a height of a foot or more and, rising from a short stalk attached to some foreign substance, begins to divide up into branches almost at once to form an irregular fan-shaped colony. In large specimens the main stem and some of the larger branches are bare, the black horny axis being exposed. On most of the larger branches, however, the coenenchym is thin and transparent. On the finer and terminal branches only is it relatively thick. From the surface of the coenenchym there project a large number of little mounds or verrucae about 3 mm. in diameter, crowded together on the terminal branches but more scattered on the larger ones. These verrucae shelter the thin transparent polyps in the retracted condition. They are usually irregularly distributed, but in some specimens in the Medi-

¹ See J. S. Thomson, *Ann. and Mag. Nat. Hist.* x., 1912, 482.

terranean Sea (regarded by von Koch as a distinct species, *G. cavolini*) they are arranged in longitudinal rows.

When alive and expanded the colonies are red, yellow, or white, but the colours fade when the colony is dried or preserved in spirit. Museum specimens are always white.

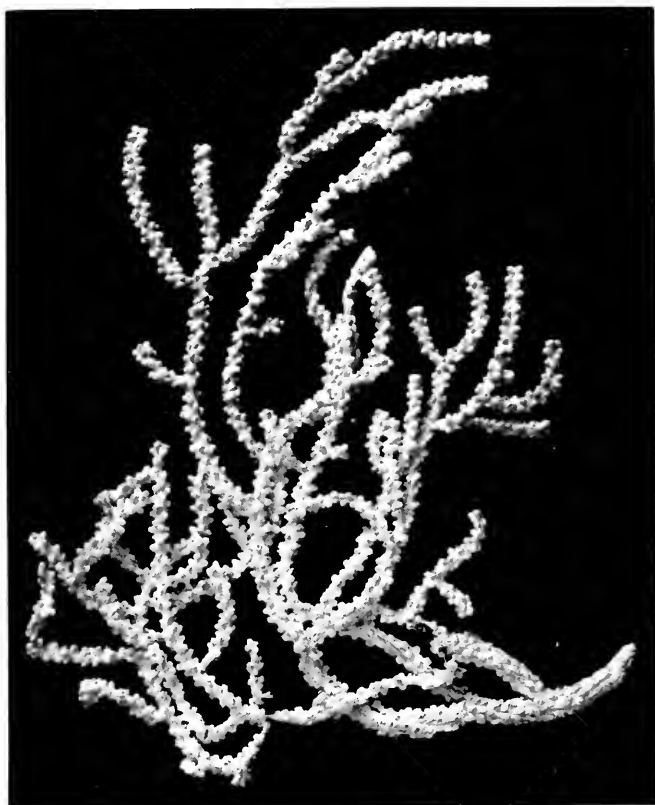


FIG. 57.—*Gorgonia verrucosa*. Part of a colony from Plymouth.

Gorgonia flammea. Among the many varieties of Gorgoniidae that are usually found in our collections there is one that calls for a few words on account of its great size and very conspicuous colour. This is the *Gorgonia* (*Lophogorgia*) *flammea*, which is found in shallow water in Algoa Bay and other localities off the coast of South Africa. It can

be recognised at once by the fact that the stems and branches are considerably flattened and by its brilliant scarlet colour. Specimens over four feet in height have been found.

In the West Indies the most conspicuous members of the family are *Leptogorgia*, *Pterogorgia*, and *Xiphigorgia*, which form great tufts of long flexible branches frequently adorned with brilliant purple, red, and yellow colour. In *Leptogorgia* and *Pterogorgia* the polyps are arranged laterally on the branches, and between them in dried specimens there is a shallow longitudinal groove. In *Pterogorgia* the polyps when retracted are protected by well-marked verrucae; in *Leptogorgia* the verrucae are very small and not raised above the level of the coenenchym. In *Xiphigorgia* the position of the polyps is indicated in dried specimens by three or four prominent ridges without verruciform swellings.

The genus *Phyllogorgia*, also found in the West Indies, is characterised by the leaf-like expansion of the branches of its flabelliform colony.

The family *Gorgonellidae* includes a large number of genera many of which have a close resemblance to the *Gorgoniidae*. The coenenchym is usually thin and the position of the retracted polyps indicated by low mounds or verrucae. The only constant difference between the two families is that the horny axis is impregnated with calcareous matter.

To determine therefore whether a given specimen is a *Gorgoniid* or a *Gorgonellid* the first test is to place a piece of the axis, thoroughly well cleaned of its coenenchym, in nitric or hydrochloric acid. If it is a *Gorgonellid* it will give off bubbles of carbon dioxide, and if it is a *Gorgoniid* it will not.

JUNCCELLA.—One of the most interesting of the *Gorgonellids* is *Juncella*, in which the long brown cylindrical axis is usually unbranched and sometimes has a length of several feet and is as thick as a finger. When fresh the axis is covered with a red or orange coloured coenenchym of

medium thickness and may be smooth or covered with numerous irregularly arranged verrucae.

Juncella has received various popular names such as Sea-rope, Sea-stalk, Sea-whip, and when stripped of its coenenchym it is used by the natives of the tropical countries in which it is found as a walking-stick and for other purposes, but it does not seem to have been used in the time of Rumphius by the Malays for medical purposes, as were so many of the other flexible corals.

Another very interesting family of these corals is the Primnoidae, in which the polyps are not retractile into the coenenchym and are protected by an elaborate mail of overlapping calcareous scales. The axis is unjointed and horny, but as with the Gorgonellidae the horny substance is impregnated with calcium carbonate.

PRIMNOA.—Most of the genera and species of this family live in deep water and are not very familiar objects in museums, but there is one species, *Primnoa reseda*, which is occasionally found in British waters and may be taken as an example of its kind for a short description.

There is a quaint description of this species in Parkinson's *Theatre of Plants* (1640), p. 1301, where it is called *Reseda marina*, or the Base wilde Rocket of the Sea: "Clusius in his sixte booke of Exotickes and sixt Chapter saith he had this at Amsterdam, and for the rarenesse, there set it forth to be of a hard woody substance, crusted over with the saltnesse of the Sea, being not the whole plant, but much of the lower parts, broken away, yet containing sundry branches, covered upwards, with sundry rough cups or vessels, hanging downewards, of a whitish ash colour, not much unlike unto the seed vessels of Reseda when they are ripe, but much lesse, and so brittle that they might be rubbed to poulder between the fingers."

From this account it will be seen that the popular English name for it, the Sea-mignonette, is one of long standing.

The branching of the colony of this species is irregularly

dichotomous and the branches are arranged more or less in one plane (Fig. 58).

A very fine specimen obtained by the *Goldseeker*¹ at a depth of 183 fathoms in the Farøe Channel was nearly

three feet in height with a spread of fourteen inches. But this specimen was exceptionally large.

The polyps are about 5 mm. in length, arranged densely and quite irregularly on a thin coenenchym, slightly curved and, as observed by Clusius, bent downwards. The polyps are protected by a number of large overlapping calcareous scales, and the disc and retracted tentacles are covered by eight smaller opercular scales (Fig. 59). There is no record of any of these polyps having been observed fully expanded, so that we have no knowledge of their appearance except in the retracted and somewhat contracted condition in which they are seen when they are brought on deck from the depths of the sea.

One of the most noteworthy features of *Primnoa*

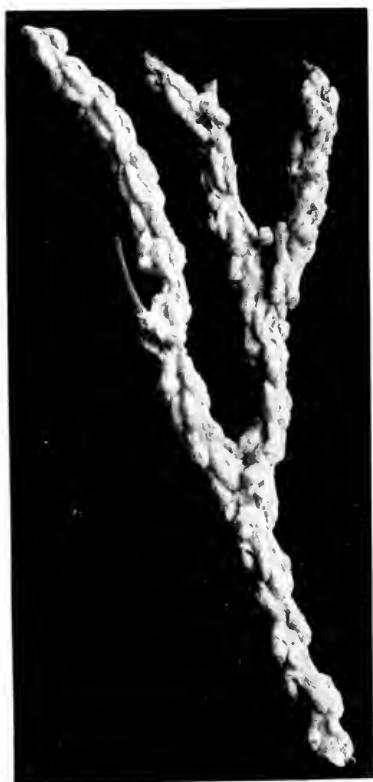


FIG. 58.—*Primnoa reseda*. A part of a large specimen. On the left of the photograph the bark has been scraped to show the horny axis. Nat. size.

reseda is the brilliant salmon-pink colour it shows when fresh, which perhaps justifies the enthusiastic comment that it is "one of the most gorgeous animals within the British area." The colour is, however, not permanent like the colours referred to in other Alcyonaria, but dissolves in the pre-

¹ See J. A. Thomson, *Proc. Roy. Soc. Edin.* xvii., 1906.

servatives or fades away if the coral is dried, and thus in the collections it has the "whitish ash colour" that Clusius describes.

Primnoa reseda is found in deep water in several localities off the west coast of Scotland, the Shetland Islands, and the Farøe Channel. It is also found in the Norwegian fjords and in the Bay of Fundy on the North American coast. It does not seem to occur in the Mediterranean Sea or in the Tropics.

There are many genera and species belonging to this family distinguished from one another by the details of the armature of the polyps and other characters.¹ The polyps are frequently arranged in regular whorls instead of irregularly as they are in *P. reseda*, and they frequently bend upwards, not downwards as they do in this species. Two species in which the polyps are thus arranged in whorls have been found in deep water off the Irish coast. Specimens of *Caligorgia flabellum*, a species with whorls of small polyps which bend upwards, were obtained from 500 - 700 fathoms, and also a specimen of *Stachyodes versluysii*, about four feet in length and unbranched, with whorls of large polyps which bend downwards, in 500 fathoms.²



FIG. 59.—*Primnoa reseda*. A small part of a branch showing the polyps covered with an armature of scales. In this genus the polyps hang downwards. . . 2 diams.

Members of the family Plexauridae, to which reference must be made, differ from the Gorgoniidae in having a thick coenenchym covering the axis, and the branches are consequently relatively thick and coarse (Fig. 60).

The axis is sometimes purely horny, but occasionally contains some calcareous granules, and at the swollen base of attachment it is frequently so densely impregnated with calcareous salts that it is as hard as limestone.

¹ J. Versluys, *Primnoidae of the Siboga Expedition*, 1906.

² Jane Stephens, *Fisheries, Ireland, Scientific Investigations*, 1909, V.

There is one more interesting feature about the Plexauridae which is very difficult to account for, and that is that in dried specimens the coenenchym is nearly always white. The colonies rarely present any of those brilliant colours which are seen in the Gorgoniidae and Gorgonellidae.

The old genus *Plexaura* has in recent years been split up into a number of genera on the ground of differences in the structure of spicules and in other characters which need not concern us now, but the principal interest of this group of genera is that the hard black axes are very largely used even at the present day by the mariners of the Indian and Pacific

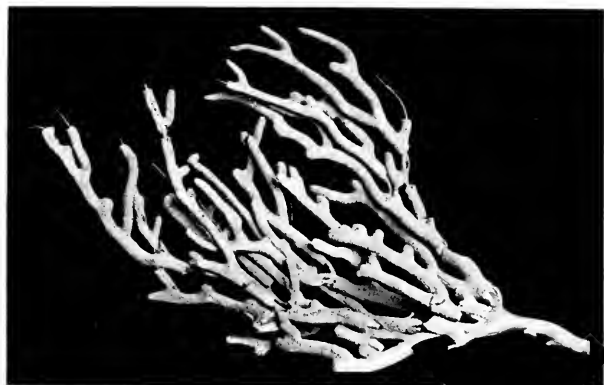


FIG. 60.—*Plexaura*. A part of a specimen from Torres Straits. Note the thickness of the bark as seen on some of the terminal branches where the horny axis projects. About $\frac{1}{2}$ nat. size.

Oceans to make into bracelets and other amulets as a protection against rheumatism and the dangers of the sea (see p. 247). There can be little doubt that the *Accarbaar itam* of the Malays mentioned by Rumphius was a Plexaurid.

It is difficult to determine with any degree of certainty what the stony rushes (*junci*) were that the soldiers of Alexander observed in the Indian seas. They may have been Gorgonians of various kinds or possibly Antipatharia, but nothing fits the description better than some of the species of the Plexauridae.

The last two families of these flexible corals do not

contain any genera that are very well known, and most of them are to be considered among the rarities of museum collections.

The Muriceidae is a very large and difficult family showing great variety in form, colour, and habit. The most noticeable character is that the surface of the coenenchym and of the polyps is usually armed with minute spines, so that it is rough or harsh to the touch. This is due to the fact that many of the spicules at the surface are relatively large and provided with spines which project through the ectoderm (Fig. 45 D, p. 105).

The Chrysogorgiidae are almost entirely confined to deep water, and are very rare. In a large proportion of the species the spicules are thin oval or hour-glass plates. This character of the spicules has suggested to some authors that the Chrysogorgiidae are the most primitive of all the Gorgonacea, but it is possible that this and other characters may be associated with the life in the slow uniform currents of deep water, and a sign of special adaptation rather than of primitive features.

CERATOPORELLA.¹—A very remarkable coral was obtained by the naturalists of the American *Blake* Expedition in 100 fathoms of water off Cuba, the zoological position of which was difficult to determine.

The single unique specimen consists of a lump of very hard limestone perforated by boring sponges in various directions. Projecting from one side of this lump there is a mushroom-shaped process capped by a thin brown lamina, circular in outline and 42 mm. in diameter, composed of short vertical tubes. There seems to be little doubt that the whole lump of coral was formed by the successive growth of the organisms that constructed the short brown tubes at the surface (Figs. 61 and 62).

¹ See Hickson on "Ceratopora," *Proc. Roy. Soc.*, 1911, vol. 84, p. 195. The name *Ceratopora*, being preoccupied, was subsequently changed to *Ceratoporella*.

The tubes are not tabulate and show no signs of septa or columella, and the corallum is imperforate. They are about 0.2 mm. in diameter and 1 mm. in length, ending below in a conical pit in the solid calcareous substance.

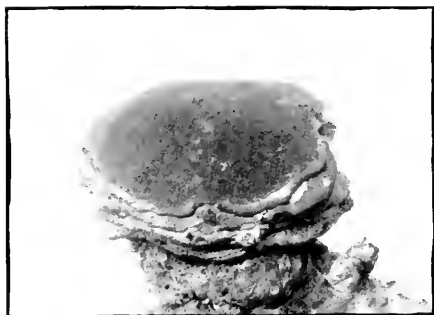


FIG. 61.—*Ceratoporella nicholsonii*. Off Cuba, 100 fathoms. Nat. size.

The only evidence there is of the affinities of this coral is afforded by the presence in the margin of the tubes of a number of slender calcareous tuberculate spicules. These spicules have a close resemblance to the spicules of some of the Alcyonaria.

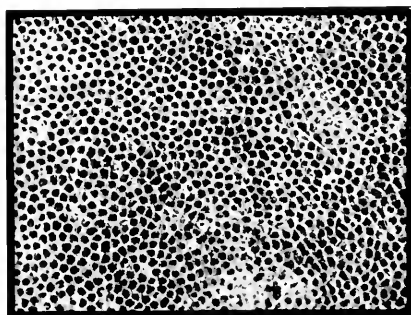


FIG. 62.—Surface view of *Ceratoporella*. $\times 10$ diams.

It must not be considered as certain that *Ceratoporella* is an Alcyonarian from this single piece of evidence, as spicules of various kinds and sizes are also formed by cal-

careous sponges, but when it is combined with a system of regular monomorphic tubes the balance of evidence turns down the Alcyonarian side of the scale.

The examples of Alcyonaria described in the preceding pages are not arranged in their zoological order, and the following table is added to indicate to the student the system of classification and the position of these examples in the group.

ORDER I.—Stolonifera. Primary polyps springing independently from a membranous or ribbon-like axis.

Tubipora.

Telesto.

ORDER II.—Alcyonacea. Colonies without an axis, spongy in texture.

Alcyonium.

Sarcophytum.

ORDER III.—Coenothecalia. Colonies without an axis, stony in texture.

Heliopora.

Ceratoporella ?

ORDER IV.—Gorgonacea. Colonies with an axis.

Sub-order A.—Pseudaxonia. Axis perforated by canals or solid and stony.

Wrightella. Corallium.

Paragorgia. Melitodes.

Sub-order B.—Axifera. Axis solid, horny, or horny and calcareous.

Gorgonia. Plexaura.

Isidella. Primnoa.

Isis. Pterogorgia.

Juncella. Rhipidogorgia.

Leptogorgia. Xiphigorgia.

CHAPTER VI

ANTIPATHARIAN CORALS

“ La principale différence que l'on observe entre les Antipates et les Gorgones, consiste dans la nature de l'écorce ; ces dernières l'offrent plus ou moins crétacée, friable et presque terreuse par la dessiccation, tandis que dans les premiers, elle est d'une consistance presque semblable à une substance gommeuse desséchée.”—LAMOUROUX, *Polypiers coralligènes flexibles*, p. 368.

THE group of the Antipatharia exhibits the same character as that of the family Gorgoniidae of the Alcyonaria in forming a hard, horny axial support which is not impregnated with calcareous matter. The Antipatharia, like the flexible Alcyonarian corals, also show a great variety in the form and method of branching. Some have a long straight or spirally twisted unbranched stem ; some branch in all directions like a shrub, others in one plane to form a fan-shaped structure. In some the branches anastomose to form a network, in others they do not. It is not, therefore, possible to distinguish with certainty the axis of an Antipathes from the axis of a Gorgoniid either by its chemical composition or by its mode of growth.

The horny axis of the Antipatharian corals, however, can usually be recognised when the finer terminal branches are examined with a lens, because they are provided with a number of sharp, thorn-like processes which give them a rough or prickly surface (Fig. 64), and on this account they were called by the older writers the Prickle corals (Stachelkorallen). It is on the arrangement of these thorns on the branches that the classification of the Antipatharia into genera and species largely depends. The main stem and

the larger branches are frequently without thorns, and present a hard, smooth, and often highly polished jet-black surface. The axis of the Gorgoniidae and Plexauridae is never provided with thorns, and although it may be grooved, always feels smooth to the touch, and the same is true of the genus *Gerardia*, which is described at the end of this chapter.

In transverse sections of a stem or thick branch of an Antipatharian coral there is usually found a central circular cavity around which the horny matter is arranged in a number of concentric layers. It has, therefore, some resemblance to a section of a tree stem, the central cavity corresponding with the pith and the concentric layers of keratin with the annual rings of wood.

In the axis of the Gorgonacea there is usually no central cavity, the texture is more fibrous than in the Antipatharia, and the concentric lamellae, if present, much less well defined.

In the large thick stems of the black coral sometimes used by the Japanese for making their elaborately carved netsukes, the central cavity and the arrangement in concentric layers may be entirely obscured, although this coral is undoubtedly Antipatharian in origin, and consequently no single character is left by which the exact nature of black coral can be determined with certainty.

The soft living tissue which covers and secretes the horny axis of the Antipatharia is absolutely different from that of any of the Alcyonarian flexible corals. It forms only a thin white or purple coloured transparent film, and is entirely devoid of spicules or any other kind of calcareous structures. This character of the soft tissues of the Antipatharia was recognised by Rumphius, Pallas, and other writers of the eighteenth and early part of the nineteenth centuries.¹ They called it slime or mucus in contrast to the coenenchym of the Alcyonaria, which they called "bark."

The polyps are small, and, with a few exceptions, are

¹ "Cortex autem, quo Antipathes vivit, non calcareus est; sed gelatinosum tegumentum in extremis ramis crassius, inque polypos efflorescens" (P. S. Pallas, *Elenchus Zoophytorum*, 1766, p. 206).

provided with only six short finger-shaped tentacles and six complete mesenteries (Fig. 63).

Provided, therefore, that some of these soft tissues are preserved, there is no difficulty whatever in distinguishing an *Antipathes* from a *Gorgonia*, but unfortunately they entirely disappear when the coral is dried, and all that usually finds its way into the hands of the collector is the bare horny axis. The axis of the stems and larger branches of *Antipatharia* were undoubtedly one of the sources of the black coral of ancient writers, which was used, as is related in another chapter, for its power of "resisting fascinations"; but it must be said that, in all probability, the Greek word *Antipathes*, which literally means an Antidote, was also

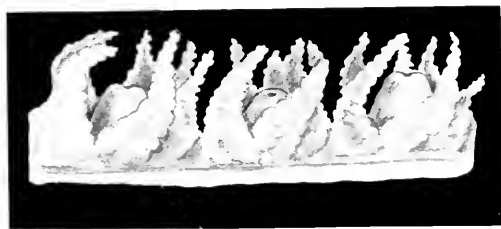


FIG. 63.—*Antipathes larix*. A small part of a branch showing three polyps each with six tentacles. $\times 20$ diams.

applied to other horny axes than those of the corals we now call *Antipatharia*.

The classification of the *Antipatharia* into families and genera has proved to be a matter of great difficulty, because the characters afforded by the axis alone are very unreliable, and the characters afforded by the soft parts are but rarely sufficiently well preserved to be trustworthy.¹ It is, therefore, a task which requires not only a great knowledge of the literature, but also skill and experience to determine with any certainty to what genus or species a given specimen belongs. This is a task which as a rule must be left to the specialist.

¹ For an excellent and thorough survey of the group the monograph by A. J. van Pesch, *The Antipatharia of the Siboga Expedition*, Livr. lxxiii., 1914, should be consulted.

To illustrate the general character of the group, reference may be made to two or three forms in which the task of identification is a comparatively simple one.

Antipathes (*Parantipathes*) *larix* is a species which has been found in deep water in the Mediterranean Sea, off the Farøe Islands, off the west coast of Ireland, in the Bay of Biscay, and also in the Sulu Sea in the Malay Archipelago.

It has a very characteristic method of branching, which has been compared with a twig of a larch tree but is more expressively termed "bottle-brush form."

In many specimens there is a central main unbranched stem attached to a stone from which spring five or six longitudinal rows of numerous long delicate branches, usually called the pinnules. The pinnules stand out at right angles to the main stem, and as they are of approxi-



FIG. 64.—*Antipathes larix*. A part of the horny axis of a branch showing the characteristic rows of thorns. 20 diams.

mately equal length they have the same kind of appearance as the bristles on a bottle-brush.

The polyps are arranged in a single row on the upper side of these pinnules, and it is not difficult to see in well-preserved specimens from Naples (Fig. 63) that each polyp possesses six tentacles, and that each tentacle bears a number of dome-shaped tubercles which are armed with stinging cells (nematocysts). There is, strictly speaking, no coenenchym, as the row of polyps is continuous, and each polyp communicates directly with its neighbours.

Unbranched specimens over one foot in height were found in 412 fathoms of water by the *Huxley* Expedition in the Bay of Biscay,¹ and a fine specimen, over three feet in height, with more than half a dozen strong branches bearing the pinnules, has been described by Professor Thomson² from the Farøes.

¹ S. J. Hickson, *Journ. Mar. Biol. Assoc.* viii., 1907.

² J. A. Thomson, *Proc. Roy. Soc. Edin.* xvii. 5, 1908.

Antipathes spiralis of the older authors is characterised by the single unbranched stem, which is twisted in a spiral fashion.

This is the *Palmijuncus anguinus* of Rumphius, and seems to have, like many other Antipatharia, a world-wide distribution. It might be mistaken for the stripped axis of one of the Juncellidae (see p. 128), but differs from it in the presence of prickles on the surface and by the absence of any calcareous matter in its composition.

Unbranched spiral specimens of *Antipathes* are now relegated to two different genera, *Cirripathes* and *Stichopathes*, which differ from one another in the arrangement of the polyps. In the former they are situated in several rows on the stem, in the latter in a single row.

Rumphius states that specimens over five feet in length were obtained in the Amboyna Sea, but specimens of *Stichopathes spiralis* taken in deep water in the Bay of Biscay and of *Cirripathes spiralis* taken off the west coast of Ireland are not more than one foot in length.

In the third form of growth, which may be described under the name *Antipathes flabellum* (Fig. 65), there is a short thick stem attached to a rock. This stem breaks up immediately into a profusion of small branches arranged in one plane, which divide and subdivide and anastomose to form a fan-shaped structure. In old times these corals were called "mourning fans" (Trauerfächer) to distinguish them from the Gorgonacean sea-fans.

In the modern system of nomenclature the fan-shaped Antipatharia are relegated to two or more genera (*Aphanipathes*, *Tylopathes*).

There are several other genera with a more irregular method of branching, but they are difficult to distinguish from one another without special study of the polyps and the arrangement of the prickles on the terminal branches. For the identification of these the recent memoirs on the group should be consulted.



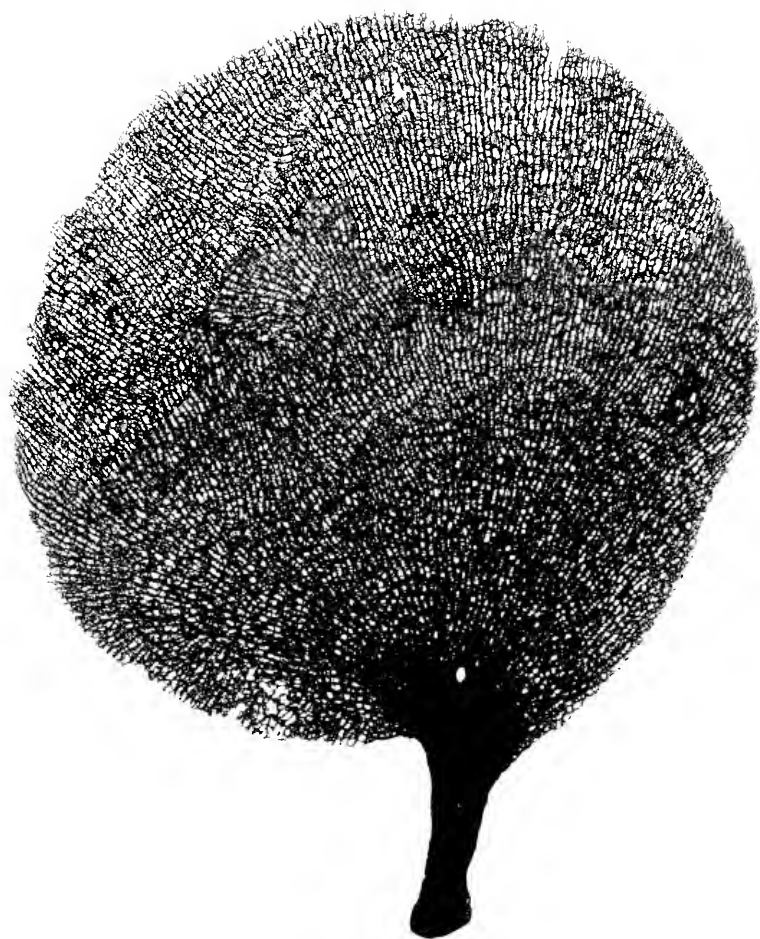


FIG. 65.—*Antipathes (Tylopathes) flabellum*. nat. size.

ZOANTHIDEAN CORALS

Gerardia savalia is the accepted name for a remarkable Mediterranean black coral which was first mentioned by Ferrante Imperato in 1599 under the name Savaglia.

From the fact that it has a black horny axis it was, until recent times, classified with the Antipatharia, but the researches of Carlgren¹ have shown that the polyps which form the axis of *Gerardia* have a different structure from the Antipatharian polyps, and resemble in essential characters those of another group of Coelenterata called the Zoanthidea. It is not necessary to give full details of the structure of these polyps, but it may be said that they have a great many more tentacles (twenty-four or more) and mesenteries than the polyps of the Antipatharia, and that when retracted they form a thicker bark or crust over the axis.

The colony is said to begin life by encrusting a stem of a *Gorgonia*, but soon surpassing its support in growth it forms a basal horny skeleton of its own and builds up very large branching colonies.

Many authors refer to the great size which specimens of this coral reach, and it is possible that *Gerardia* was the principal source of the black coral that was used by the Mediterranean races in early times.

A specimen, now in the British Museum, that was dredged up from a depth of 20 fathoms of water off the Grecian island of Negropont, is $6\frac{1}{2}$ feet in height and has an expanse of 6 feet 8 inches. The main trunk from which the branches arise is 1 foot 5 inches in circumference.²

The anatomy of *Gerardia* was first described by de Lacaze-Duthiers,³ who gave some beautiful illustrations of the anemone-like polyps when fully expanded. The colour of the polyps is said to be normally a greenish-yellow, but at the time when they are charged with reproductive bodies this colour, as well as the usual transparency of the tissues, may be obscured by the brick-red eggs or the white testes.

¹ Carlgren, *Ofvers K. vet. Akad.*, 1895, 5.

² F. J. Bell, *Trans. Zool. Soc.*, London, 1891, p. 87.

³ De Lacaze-Duthiers, *Ann. Sci. Nat.* (5), ii., 1861, p. 169.

The axis of *Gerardia* consists of a series of concentric lamellae of black horny substance, but the lamellae appear to be more firmly cemented together than is generally the case in the *Antipatharia*. In the centre of the axis there is usually found a core of a substance which is not formed by the *Gerardia*. This may be the stem of a Gorgonian coral or some other structure which the *Gerardia* has covered by encrustation in the early stages of its growth.

The surface of the axis is smooth to the touch, as it does not possess the prickles or spines which form such a characteristic feature of the axis of the branches of the *Antipatharia*. But when the surface is examined with a magnifying glass it is found to be covered with a number of little pitted mounds (*mamelons ombiliqués*).¹

So far as is known at present the genus *Gerardia* is confined to the Mediterranean Sea. The large specimen in the British Museum came from Grecian waters, but specimens of great size are also obtained by the coral fishers on the coast of Algeria and Tunis.

¹ According to de Lacaze-Duthiers, *l.c.* p. 216.

CHAPTER VII

HYDROZOAN CORALS

"When a Writer acquaints me only with his Thoughts and Conjectures, without enriching his Discourse with any real Experiment or Observation, if he be mistaken in his Ratiocination, I am in some Danger of erring with him, or at least am like to lose my Time, without receiving any valuable Compensation for so great a Loss; but if a Writer endeavours by delivering new and real Observations and Experiments to credit his Opinions, the Case is much otherwise: for let his Opinions be ever so false I am not obliged to believe the former, and am left at Liberty to benefit myself by the latter; and though he have erroneously superstructed upon his Experiments, yet, the Foundation being solid, a more wary Builder may be much farthered by it, in the Erection of a more judicious and consistent fabrick."—Mr. BOYLE, quoted by H. Baker, *l.c.* p. 206.

THE polyps of the Hydrozoa, although presenting an external appearance very similar to that of the polyps of the other Coelenterata, are much simpler in structure.

There is normally a mouth surrounded by a crown of tentacles varying in number in the different genera of the group, but always filiform or digitiform in shape and without lateral pinnules, but the mouth leads directly into the body cavity and there is no stomodaeum and no mesenteries.

Most of the genera of Hydrozoa form colonies by gemmation, which are attached to the rocks or sand by root-like processes, and, by various methods of ramification, give rise to plant-like structures of considerable size.

By the older naturalists they were included in that strange medley of marine products called the Zoophytes.

Before passing on to the description of the Hydrozoa that form calcareous structures there are two morphological

features of the group to which a passing reference must be made.

In many of the colonies it is found that the polyps are not all alike but present two or more different kinds adapted for different purposes. One of the commonest forms of this dimorphism is seen in the two Orders of Hydrozoan corals which will be described in this chapter. It consists in the reduction of the tentacles of the one kind, called the gasterozooids, so that they become little more than a mouth and digestive tube, and in the loss of the mouth and digestive functions in the other kind, called the dactylozooids, which become elongated, flexible, and active for catching food by means of the numerous batteries of nematocysts with which they are armed.

The second feature of importance concerns the origin and position of the ovaries and testes. These organs are always situated in the outer layer of the body wall, and their products when ripe are always discharged directly into the sea and never pass through the body cavity as they do in the Orders of Coelenterata that have been described in previous chapters. Sometimes these genital organs are found on the body wall of ordinary Hydrozoan polyps, but in many other cases they are only borne by specially modified zooids called the medusae, which become detached from the parent colony and swim away to distribute their sexual products in the open sea.

The medusae are little jelly-fish having a very different appearance from the sedentary polyps of the colony. They have the form of minute umbrellas with usually a ring of tentacles round the margin, and for a handle a short process called the manubrium, at the end of which is situated the mouth.

In some cases the medusa undergoes degeneration, losing its principal characters, and never succeeds in becoming detached from the parent colony. The story of this degeneration is one of extreme interest to the zoologist, but it has no bearing on the problems dealt with in this book.

There are two Orders of the Hydrozoa that may fairly be called Corals. These are the Milleporina and the Styla-

sterina. In many text-books of zoology they are still grouped together to form the Order Hydrocorallinae, but although they have in common the two characters of dimorphism and a massive calcareous corallum, the structure of the polyps and of the reproductive bodies suggest that the resemblances between the two groups are due to convergence rather than to genetic affinity.

The Order Milleporina is constituted for only one genus—*Millepora*—which has a wide distribution in the warm shallow waters of the East and West Indies. It was A. Agassiz in 1859 who first proved that the correct position of the genus is in the class Hydrozoa, but Moseley's brilliant researches during the voyage of H.M.S. *Challenger* in 1876¹ provided us with the first correct account of its general structure.

The corallum assumes many varieties of form. Sometimes it consists of thick massive plates, sometimes it is coarsely branched or becomes profusely ramified. These differences in form seem to be associated with differences in the conditions of the immediate environment and cannot be used as characters for specific distinctions.

The special characters of the corallum can be easily recognised with the help of a simple magnifying glass. The surface is perforated by a very large number of pores, and these pores are of two sizes, the larger or gastropore (about 0.25 mm. in diameter) and the smaller or dactylo-pores (about 0.15 mm. in diameter) (Fig. 66).

When examined in sections these pores are seen to lead into delicate tubes which pass radially towards the centre of the branch, and each tube is divided into a number of chambers by very thin transverse partitions called the tabulae (Fig. 67, Tab.). Between the tubes the corallum is seen to be perforated by a dense plexus of branching canals. On account of its porous texture *Millepora* was named by Rumphius *Lithodendrum saccharaceum album*, or the White Sugar Coral.

The corallum is therefore perforate, tabulate, and provided with dimorphic pores.

¹ H. N. Moseley, *Challenger Reports*, vol. ii., 1881.

In many specimens, and particularly in the older parts of the corallum, the pores are arranged in circles—called the cyclo-systems—a single gasteropore in the centre of the circle and a ring of five to seven dactylopores around it. At the growing edges of the fronds or branches and all over the surface of some specimens the pores seem to be much more irregularly scattered. The arrangement of the pores in cyclo-systems must not, therefore, be regarded as an in-

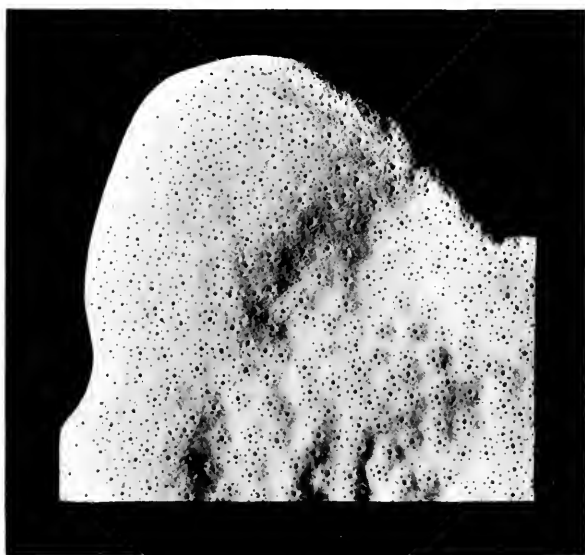


FIG. 66.—*Millepora*. A part of a frond of a large colony, showing the pores arranged in regular cyclo-systems. Nat. size.

variable character of the corallum of *Millepora*. Occasionally there may be found in museum collections specimens of the coralla of *Millepora* which look as if they were afflicted with a disease or were otherwise abnormal (Fig. 68). They exhibit all over the surface, or on some parts of it only, a number of shallow, blister-like cups having a diameter about twice that of the gasteropores. These cups are the Ampullae, and it is now known that they are the receptacles of the medusae which bear the eggs or sperms.¹ They are

¹ S. J. Hickson, *Proc. Roy. Soc.*, vol. lxvi., 1899.

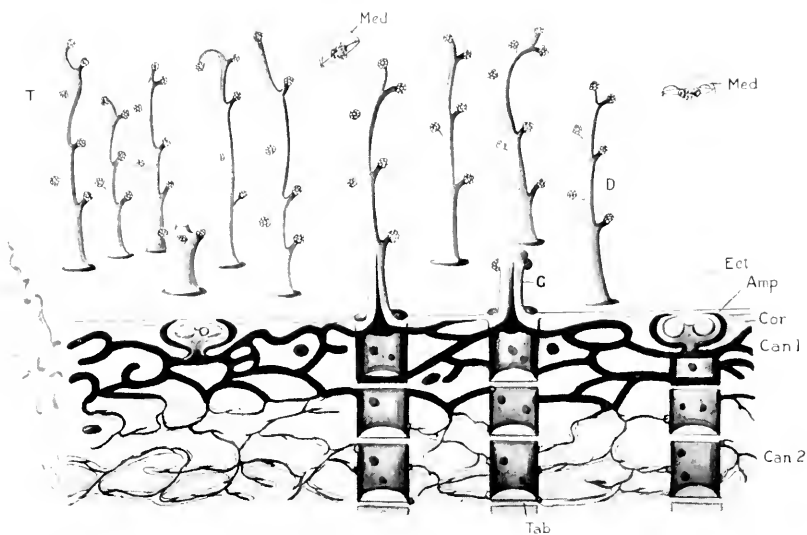


FIG. 67.—Diagram of a living *Millepora*, showing Amp., an Ampulla with a medusa enclosed in it; Can. 1, the living canals; Can. 2, the dying and degenerating canals; Cor., the Corallum; D., the Dactylozooids; Ect., the external sheet of Ectoderm; G., the Gastrozooids; Med., the free swimming Medusae; Tab., the Tabulae. Slightly modified from Moseley and the *Cambridge Natural History*.

not always present ; in fact, specimens of the kinds shown in Fig. 68 may be regarded as rarities in our collections, for, unlike many other Hydrozoa, *Millepora* does not produce its medusae continuously or over a long period of time, but so far as we can judge only occasionally and then in great profusion. But our knowledge of the periodicity of medusa production in *Millepora* in any part of the world is still lacking in precision.

Passing now to the structure of the living tissues which form the corallum we find that there are two kinds of polyps—the gastrozooids and the dactylozooids—inhabiting the gastropores and dactylopores respectively. The gastrozooids are short and stumpy polyps projecting only a little way above the surface of the corallum when fully extended (Fig. 67, G.). They have a terminal mouth and a digestive cavity, in which occasionally a small crustacean may be found as food, and round the mouth are four knobs, armed with nematocysts, which probably represent four rudimentary tentacles.

The dactylozooids (Fig. 67, D.) when fully extended are long, slender, hollow structures provided with a variable number of short capitate tentacles arranged alternately or more irregularly on the body wall. They have no mouths. There can be no doubt that the function of the dactylozooids is to catch and paralyse the small living organisms that come within their reach and to pass them to the gastrozooids to swallow and digest—an admirable example of efficient division of labour. The zooids are connected together beneath the surface by an elaborate system of branching and anastomosing coenosarcial canals. These canals are provided with a double lining of cells. The outer layer of cells—the ectoderm—is mainly concerned with the secretion of the calcium carbonate that forms the corallum. The inner layer of cells—the endoderm—may serve the purpose of providing the ciliary action necessary for the maintenance of the circulation of currents of water through the canals, but on that point further investigation on living material is needed. The most striking feature of the canal system is the presence, in enormous numbers, of the symbiotic

organisms called zooxanthellae, the function of which has been discussed in a previous chapter (p. 20).

The coenosarcral canals are confined to the outermost layer of the corallum. Down to the level of the first tabula (Can. 1 in Fig. 67) they are alive and functional; below that, for a distance represented by two or three tabulae, they are shrivelled and degenerating, and below that again they disappear altogether.

Thus when a branch of a *Millepora* preserved in spirit, say half an inch in diameter, is treated with acid and the corallum dissolved away, the whole system of canals and polyps is represented by a film not more than $\frac{1}{10}$ of an inch in thickness.

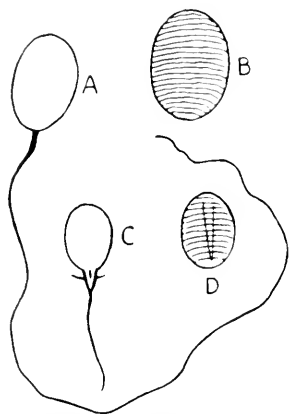


FIG. 69.—The nematocysts of *Millepora*. A, The large kind with the thread discharged. B, The same before discharge. C, The small kind with thread discharged. D, The same before discharge. $\times 700$ diams.

The colonies of *Millepora* are richly supplied with nematocysts, and as some of them are powerful enough to pierce the human skin, causing a painful form of nettle-rash, the *Millepora* is regarded as a stinging coral. The nematocysts are of two kinds: a smaller kind found in the tentacles of the zooids, armed with four sharp spines at the base of the filament, and a larger kind without spines but with a much longer filament which are scattered over the surface of the

coenenchym between the zooids (Fig. 69).

The reproduction of *Millepora* is of extraordinary interest, because it presents us with the only example that is known of a stony coral that produces free-swimming medusae. The medusae are produced in great numbers, they are of a very simple structure, and when a colony is examined, are found to be of the same sex, either male or female, and at approximately the same stage of development.

There are many points about this production of medusae in *Millepora* on which we are still in ignorance. It is not

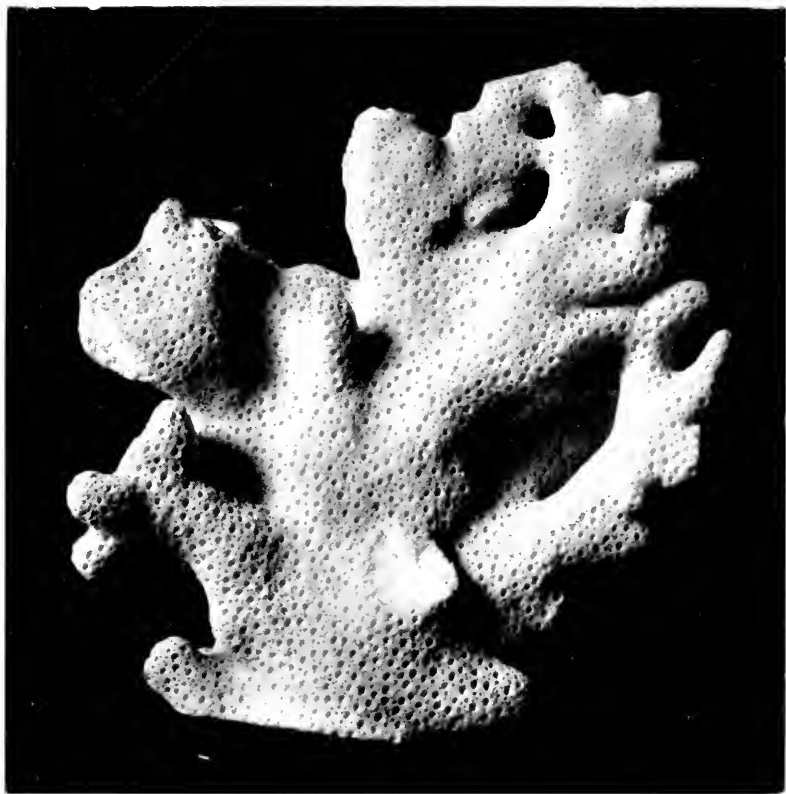


FIG. 68.—*Millepora*. A part of a colony showing the surface profusely pitted with ampullae. Nat. size.

known, for instance, whether they are produced periodically or spasmodically, or whether their production is due to environmental conditions that affect all the Millepores of the reef at the same time, and it is also not known at what size or age they first begin to produce medusae.

All that can be said at present is that when the collections of corals in museums are examined very few specimens are found that exhibit the ampullae in which the medusae are lodged, and this suggests that the phenomenon occurs at long intervals of time and does not last long.

The medusa consists of an umbrella and a short stumpy manubrium, which is, in some cases, provided with a mouth in the female medusae but never in the male (Fig. 67, Med.). The umbrella is extremely thin, and bears neither radial nor ring canals. Close to its margin there are four or five knobs, each one consisting of a battery of nematocysts, but apart from this there are no tentacles. In the ripe female medusae four or five relatively large yolk-laden eggs are borne by the manubrium. In the ripe male medusae the testis is in the form of a ring round the manubrium. The size of the medusa in both sexes is about 0.4 mm.

It is very improbable that the medusae have a long free-swimming life, and Mr. Duerden has observed that the female medusae discharge their eggs within five or six hours of their liberation.

Although *Millepora* occupies such an isolated position in the animal kingdom, for it has really no near relation among the corals, there is no evidence that it had made its appearance on the reefs even as late as the Tertiary geological period. It is true that a number of corals which have been given the name *Millepora* by various authors are found in the Tertiary and even older rocks, but a careful examination of these fossils shows that not one of them possesses the very distinctive characters of the corallum of *Millepora*.

The only fossil coral that approaches *Millepora* in structure is the genus *Axopora* from the Eocene of France, but this coral has monomorphic pores and each pore bears in its centre a minute spine or columella.

Millepora is a common constituent of the coral reefs of

the world, but it has been found also in depths of 20 to 40 fathoms off the Maldives.¹

THE ORDER STYLASTERINA. — The second Order of Hydrozoan corals is called the Stylasterina, and it is represented by two common and widely distributed genera—*Distichopora* and *Stylaster*—and several others of rarer occurrence.

As in *Millepora*, there is a massive corallum of calcium carbonate which is perforated by a plexus of canals, and there are two kinds of pores—the gasteropores and the dactylopores. In the common genera mentioned above, the corallum can easily be distinguished from that of *Millepora* by the presence of styles in the gasteropores, and by the absence of tabulae. In some of the deep-sea genera, however, there are no styles, and tabulae are occasionally present in the gasteropores. The style is a little calcareous column, usually covered with minute tubercles and spines, which is situated in the centre of the pores like the columella of a Madreporarian coral (Figs. 71 and 72).

The gastrozooids of the Stylasterina resemble those of *Millepora*, except that the endoderm is reflected over the style so as to provide more digestive surface, and each gastrozooid has a mouth and four short tentacles. The dactylozooids, on the other hand, differ very markedly from those of *Millepora* in being very short, in having no tentacles, and in possessing a scalariform endoderm which entirely blocks up the cavity. The plexus of canals which forms the coenenchym is not so close as it is in *Millepora*, and the living tissues penetrate much deeper down into the substance of the corallum. The nematocysts are very small and simple in structure, and are confined to the tentacles of the gastrozooids and the ectoderm of the dactylozooids. There are no nematocysts at the surface of the coenenchym.

The Stylasterina do not produce free-swimming medusae, but the eggs and sperms are formed in ampullae. In each ampulla there may be one or more cups of folded endoderm called the trophodiscs, each of which supports and nourishes

¹ J. Stanley Gardiner, *Fauna and Geography of the Maldives and Laccadive Archipelagoes*, vol. i. part 3, p. 325.

either a testis or a simple large yolk-laden egg, or it may contain a larva and a withered trophodisc. The trophodisc is sometimes provided, in the male, with a central column of endoderm, called the Spadix, which resembles the manubrium of a medusa, and by some authors the trophodisc is regarded as a degenerate medusa. This is, however, a matter that requires further investigation.



FIG. 70.—*Distichopora*. Surface view of a branch showing the ampullae.
× 2 diams.

The ampullae can usually be seen at the surface of the corallum and have the appearance of a cluster of blisters each about 0.5 mm. in diameter (Fig. 70); and in all the genera that have been examined, sexual reproduction appears to be continuous, the gonophores in various stages of development being found in nearly all the full-grown specimens. The sexes are usually separate. Very seldom does a colony

produce both male and female gonophores at the same time. Only one case of hermaphroditism has been recorded in *Distichopora*.¹ The eggs are fertilised and undergo the early stages of their development within the ampullae, and when the female ampulla bursts, there emerges a free-swimming planula larva. The *Stylasterina* are therefore viviparous.

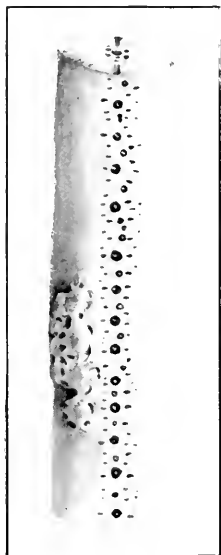


FIG. 71.—*Distichopora*. Edge view of a branch showing the arrangement of the gasteropores in a median line; the dactylopores on each side of them. On the left may be seen a cluster of ampullae. 2 diams.

DISTICHOPORA.—The genus *Distichopora*, formerly known as red or violet sugar coral (Rumphius) or *Millepora violacea* (Pallas), forms a flattened, flabellate, and sparsely branched corallum rarely exceeding 4 or 5 inches in height and is almost invariably brightly coloured (violet, red, orange, or brown). The pores are situated on the edges of the branches in three rows, a middle row of gasteropores flanked on each side by a row of dactylopores (Fig. 71). In some places the rows of pores pass on to the flat sides of the branches for a short distance. The ampullae are seen in clusters, sometimes on one only, sometimes on both sides of the flat surfaces of the corallum (Fig. 70). When a branch is examined in section, and for this purpose a section made in the plane of the pores is the best, each gasteropore is seen to be provided with a long, slender style. The pores have a long curved course and penetrate almost to

the centre of the branch, but they are not, as a rule, divided into partitions by tabulae.

Distichopora may be found in rock pools and in shallow sea water in the tropical regions of the old world and in the West Indies. A few specimens have also been found in deeper water in the West Indies (100-270 fathoms) and in the Indian Ocean (150 fathoms).

¹ H. M. England, *Trans. Linn. Soc.* xii., 1909, p. 347.

STYLASTER.—The other genus of Stylasterina that is very common is Stylaster. This coral forms profusely branched flabellate colonies which sometimes attain to a great size and when found in shallow water often possess such a beautiful rose-pink colour that they are used for ornamental purposes. The older branches of these Stylasters are very hard and are frequently mistaken for the precious coral, but as they are perforated by the pores and by the canal system they do not readily take a smooth polish and are consequently of little value as jewels or charms.

This coral can be distinguished from the precious coral by two characters. In the first place, the branches are far more numerous and terminate in very delicate twigs which may be only 2 mm. in diameter. In the second place, there can be found densely clustered on the terminal branches, and more sparsely on the larger ones, a number of cyclo-systems.

These pore-cycles in Stylaster are frequently raised on a little prominence above the general surface of the corallum, and when examined with a magnifying glass exhibit a number of radially arranged ridges which have a striking resemblance to the septa of a Madreporarian coral. When the pore-cycles are prominent in this way they are usually called "calices," although there is no true homology between the calyx of a Stylaster and the calyx of a Madrepore (Fig. 72).

In each of these calices there is a centrally placed pore—the gasteropore—and close to the margin a circle of ten or more dactylopores. In each of these pores there is a short tuberculated style which has a very rough resemblance to a shaving brush. The ampullae can be seen as rough excrescences between the calices in almost every specimen that is examined.

Stylaster is a genus with an extraordinarily wide geographical distribution. It is found in shallow water in most of the tropical seas and in the deeper waters as far down as 900 fathoms. The deep-sea species are usually white, and the calices are situated on one surface only of the flabellum.

ALLOPORA.—Closely related to Stylaster is the subgenus Allopورا, which is found in the deep fjords of Norway and British Columbia, and in 50 fathoms off the Cape of

Good Hope. As in *Stylaster*, both the gasteropores and the dactylopores are provided with styles, but the calices are not so prominent, the ampullae are inconspicuous, and the terminal branches relatively thick and blunt.

Allopora nobilis of the Cape is the largest and most



FIG. 72.—*Stylaster*. A small part of a branch highly magnified to show the cyclo-systems. Note the styles in the centrally placed gasteropore and in the surrounding dactylopores. $\times 20$ diams.

robust of all the *Stylasterina*. It seems to construct great submarine forests in some localities which effectually prevent successful dredging, as the great solid stems, over an inch in diameter, are firmly fixed to rocks on the bottom.

ERRINA.¹—Of the remaining genera, *Errina*, with its

¹ S. J. Hickson, "The genus *Errina*," *Proc. Zool. Soc.*, 1912, p. 876.

two sub-generic forms *Labiopora* and *Spinipora*, appears to be the most widely distributed. The pores are not arranged in this genus in regular cyclo-systems, but are more or less irregularly scattered over the surface of the branches. The characteristic feature, however, is that some of the dactylozooids, or all of them, are protected by blunt processes of a cylindrical shape with a deep slit down one side, called by Moseley the "nariform processes." A better name for them, perhaps, is grooved spines (Fig. 73).

Each gasteropore is provided with a short "shaving-brush" style, but, as in *Distichopora*, the dactylopores have no styles.

The genus is very widely distributed in water of from 100 to 500 fathoms in depth, and recently some beautiful coloured specimens have been found in shallow water off the South Island of New Zealand, off Cape Horn and the coast of Chili, and in the Antarctic Seas.

SPORADOPORA is a rare genus from deep water, which has close affinities with *Distichopora*, but it is of special interest, because it has superficial resemblance to a ramose colony of *Millepora*, the colour being white, the texture of the corallum being more spongy and brittle than in most *Stylasterina*, and it has pores scattered irregularly over the surface. Moreover, the resemblance is accentuated by the fact that there are usually a few well-marked tabulae in the gasteropores.

The structure of the polyps and the gonophores, however, prove conclusively that *Sporadopora* is not, in any sense, a connecting link with the *Milleporina*.

The remaining genera are of comparatively rare occurrence, and the only point of special interest about them is the remarkable lamina or scale which protects the cyclo-system in the genus *Cryptohelia*.

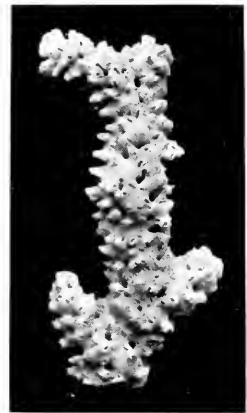


FIG. 73.—*Errina* (*Labiopora*) *aspera*. Note the characteristic grooved spines protecting the dactylopores. 5 diams.

The following table may be of assistance in identifying the genera of the Stylasterina :

A. Pores irregularly scattered—

(a) With styles in the gasteropores :

(1) Dactylozooids unprotected *Sporadopora*.

(2) Dactylozooids protected by
grooved spines *Errina*.

(b) Without styles *Pliobothrus*.

B. Pores arranged in rows *Distichopora*.

C. Pores arranged in cyclo-systems—

(a) With styles in gasteropores and
dactylopores *Stylaster*.

(b) Without styles :

(1) Cyclo-systems protected by a
lamina *Cryptohelia*.

(2) Cyclo-systems unprotected *Conopora*.

Allopora is now regarded as a sub-genus of *Stylaster*, characterised by having relatively thick, blunt, terminal branches, and less prominent calices and ampullae.

Steganopora and *Astylus* have only been recorded once from deep water. The former is closely related to *Pliobothrus*, the latter to *Conopora*.

Labiopora and *Spinipora* are sub-genera of *Errina*.

CHAPTER VIII

POLYZOAN CORALS

“Experiment is the Test of Truth, and that should always be made before we wholly assent or dissent. But if Facts come well attested by Persons of Judgment and Credit, however extraordinary they may seem they deserve civil Treatment till they be examined fully.”
—HENRY BAKER, *l.c.* p. 215.

THE group of animals known by the names of Polyzoa or Bryozoa affords several examples of skeleton formation that leads to the construction of ramified, massive, or encrusting calcareous and coral-like growths.

The polyps, or “zooids,” as they are more usually called, which construct these structures are so widely separated from the polyps of the Madreporarian corals in structure and development that, on morphological grounds, objections may be raised to their consideration in any treatise with the title of “Corals.” But the fact remains that some of the Polyzoa do form calcareous skeletons resembling corals so closely that they will continue to be called corals by many people who are interested in marine zoology but possess no expert knowledge of the groups.

In many cases it is quite an easy matter to determine whether a given specimen of coral has or has not been produced by a colony of Polyzoa, but there are others in which a very careful examination with a strong magnifying glass is necessary before the determination can be made with certainty.

There are, however, still some corals, both recent and fossil, of which there are only the hard skeletal parts to serve as a guide ; these have been attributed to the Polyzoa,

but may have been formed by the zooids of some other group of animals. It must be admitted, therefore, that, although in most cases the structure of the dried Polyzoan coral is sufficient to determine definitely that it is a Polyzoan, there are some of them which exhibit no characters of the skeleton that can be regarded as conclusive of their zoological affinities.

The only definite proof that a given coral is a Polyzoan must be obtained by an observation of the structure of the polyps which construct the coral, and a few words must therefore be written to explain the essential features of the anatomy of this group of animals.

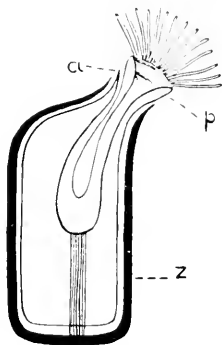


FIG. 74.—Diagram to illustrate the structure of a Polyzoan polyp. *p.*, the protrusible part of the polyp with a crown of tentacles surrounding the mouth; *z.*, the thick outer wall of the non-protrusible part of the polyp or zoecium, which is frequently calcareous; *a.*, the anus. The bent alimentary canal is seen leading from mouth to anus and attached to the base of the zoecium by a band of muscles.

When an expanded living colony of a Polyzoan is examined, the polyps are seen to protrude and to display a crown of long ciliated tentacles arranged to form a funnel, at the base of which is a centrally placed mouth (Fig. 74). By such characters they might be mistaken for Coelenterate polyps, but further examination reveals a second opening just above the crown of tentacles, and a bent tube or alimentary canal is seen through

the transparent body wall which connects these two openings to the exterior. The presence of this complete alimentary canal is quite sufficient to distinguish the Polyzoan polyps from the polyps of any other group of animals that form corals, but there are many other anatomical characters, which it is not necessary to describe in this book, by which the Polyzoa differ from other coral-forming organisms, and exhibit what is usually regarded as a much higher type of organisation.

It is rarely possible to get the chance of seeing these corals alive and expanded, but specimens which have been preserved in spirit and examined in thin sections or in slices cleared in oil usually show the essential characters quite distinctly.

The body wall of the polyp may be divided into two regions, one of which is always thin and usually transparent and is capable of being protruded with the tentacles, and the other, which is thick and opaque and is connected with the other polyps of the colony. The latter region forms a receptacle called the "zooecium" into which the expansible part of the polyp can be withdrawn telescopically for protection, and it is this part which secretes the calcareous substance in the Polyzoa described in this chapter. The outer wall of each zooecium is perforated by a large aperture through which the polyp protrudes in expansion, and this is called the "orifice," and may also be perforated by a variety of other smaller apertures according to the genus and species under observation. In many forms the orifice is not flush with the surface of the zooecium, but mounted on the end of a short spout-like projection which may be called the "collar."

There are no solitary calcareous Polyzoa, but every species consists of a colony of many polyps whose zooecia, firmly adherent to one another, build up the various kinds of branching, net-like, or encrusting structures of the Polyzoan corals.

Most of the calcareous Polyzoa form little tufts of very delicate branches or thin spreading plates on shells or stones, and the term "corallines" is more generally applied to them than "corals," but it is just as impossible to give a scientific definition of the former as it is of the latter. All that can be said is that when the word "coralline" is used it has reference to something smaller or more delicate in structure than what are commonly called "corals."

The Polyzoa are classified as follows :

Sub-class 1. Entoprocta.

,,	2. Ectoprocta	{	Order 1. Phylactolaemata.
		,	2. Gymnolaemata.

The Order Gymnolaemata is again divided into three Sub-orders :

- Sub-order 1. Cyclostomata.
- „ 2. Cheilostomata.
- „ 3. Ctenostomata.

Of the various groups into which the Class is thus divided, only two Sub-orders, the Cyclostomata and Cheilostomata, provide examples of Polyzoa with calcareous walls. In the others the walls of the zooecia are either horny, mucilaginous, or free from any protective secretion.

CYCLOSTOMATA.—The coral structures formed by the Cyclostomata usually consist of calcareous tubes with a single circular orifice at the terminal extremity. These tubes are usually closely bound together in bundles for the greater part of their course, and in some genera the bundles of tubes become so densely calcified that their tubular nature cannot be determined by superficial examination, although it is indicated by the end which bears the orifice projecting freely on the surface of the zooecium, and it can be readily seen in transverse or longitudinal sections of the main branches of the colonies.

CRISIA.—One of the commonest and most widely distributed of the Cyclostomata is the genus *Crisia* (Fig. 75). On our own coasts little bushy tufts of *Crisia eburnea* are often found attached to the zoophytes and seaweeds that are cast up on the beach after a storm. They are not more than one inch in height, and when seen by the naked eye might be mistaken for the alga *Corallina officinalis* (see p. 207). An examination with a low-power magnifying glass at once reveals their fragile tubular structure, and the large round orifices of the zooecia enable the naturalist at once to separate it from the coralline Algae.

In the species referred to, the branches are composed of tubular zooecia arranged alternately right and left, and almost entirely adnate, the orifices being only slightly raised from the surface on short tubular projections.

An important feature of the genus is that at intervals in the course of the branches the hard calcareous structures

are replaced by thin horny joints. It is extremely interesting to find in this group the same "admirable contrivance of Nature" of hard and soft joints for resisting the violent motions of the sea that has already been mentioned as occurring in some of the Alcyonaria (p. 121), and will also be recorded in the Gymnolaemata (p. 172) and in the chapter on Coral Algae (p. 207). It cannot for a moment be suggested that the Polyzoa are genetically related to the Alcyonaria or to the coral Algae, and therefore we must consider that this admirable contrivance has been attained independently in the course of evolution and forms a fine example of the principle of "convergence" in Nature.

There is just one more feature of interest in the structure of the *Crisia* colony to which reference may be made in passing, as it is characteristic of the Cyclostomatous Polyzoa.

On some of the branches of the colony a swollen pear-shaped body may be seen which has the appearance of a distorted or abnormal zooecium (Fig. 75, OV). This

is an "ooecium" or "ovicell," and is formed for the protection of the embryos. Ovicells also occur in the Cheilostomatous Polyzoa, but they are not usually so conspicuous as they are in the Cyclostomata.

In the family Tubuliporidae the colonies usually form little encrusting masses and spreading branches adherent to foreign objects, but, if erect, as some of them are, they do not exhibit the horny nodes seen in the genus *Crisia*.

The delicate fragile branches and the small size of most of the genera of the Cyclostomata give them an appearance

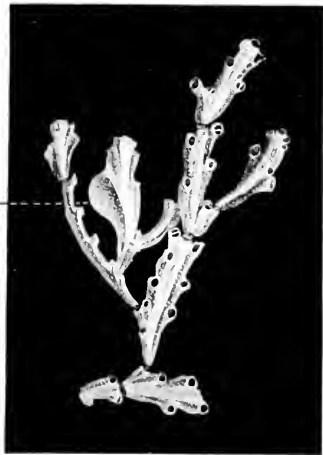


FIG. 75.—*Crisia eburnea*. A small fragment of a colony. OV, an ooecium. $\times 25$ diams.

which would be described in the language of popular natural history as "coralline" rather than "coral."

HORNERA.—In the genus *Hornera* (Fig. 76) the principal branches are much more solid, and, owing to the abundance of the calcareous secretion, the greater part of the tubular zooecia are said to be "immersed," that is to say, the outlines of the tubes are not visible at the surface. The result of this is that the colony as a whole has a much more "coral-like" appearance than the others. The colonies are erect,



FIG. 76.—*Hornera lichenoides*. Terminal branch of a specimen from off the Shetland Islands. View of the side on which the zooecia open. \cdot 7 diams.

profusely branched, and frequently fan-shaped or flabelliform. When examined with a lens the little spout-like collars, from which the zooids protrude, are seen to be arranged on one side of the branches only, and thus the fan-shaped colony may be said to have a proper or anterior surface and a reverse or posterior surface. This arrangement of the zooids on one surface only of a fan-shaped corallum is not confined to the Polyzoa but occurs in some of the Stylasterina and Madreporaria that live in deep water, and may be due to the tendency of the zooids as they are formed to turn towards the source from which the food supplies come to them. In shallow sea-water,

where the corals are subject to the ebb and flow of the tides, the food comes to them first from one side and then from the other, and the zooids are usually arranged on all sides of the branches, but in deep water there is frequently a prevailing current in one direction and the zooids become grouped on one side so as to face it.

On the terminal branches of *Hornera* the outlines of the zooecia are faintly indicated (Fig. 76), but the older branches have a much smoother coral-like surface owing to the zooecia becoming immersed by the increase of calcareous deposit.

There are no horny nodes in *Hornera*, and consequently the corallum is perfectly rigid.

The two species of this genus which occur in the British area are seldom more than an inch in height and occur in deep water (20-200 fathoms) attached to other corals and foreign objects.

The particular interest of the genus is that it is one of the many corals that were referred by Linnaeus and the earlier writers to the genus *Millepora*, and was called by him the *Lichen millepore* on account of its resemblance to his *Lichen fruticulosus seu foliaceus*. The genus *Millepora* is much more restricted now than it was in the time of Linnaeus, when it served as a receptacle for any kind of coral whose affinities could not be more accurately determined. No naturalist of modern times would refer *Hornera* to the *Milleporina*, but there is a certain resemblance to be seen between some forms of *Hornera* and the *Stylasterine* genus *Errina* (see p. 154), and there can be little doubt, judging from the excellent drawings which illustrate their memoir, that the species described by Jullien and Calvet¹ as *Hornera verrucosa* is really a species of the genus *Errina*.

HETEROPORA.—The genus *Heteropora* has been the subject of a good deal of controversy and has been mistaken for a *Millepora*. It has now been definitely identified as a *Polyzoon*, and its affinities are probably with the *Cyclostomata* rather than with the *Cheilostomata*.

It consists of a broad attached base from which a number of short dichotomously branched stems arise which end bluntly. A large specimen may be 4 or 5 inches in diameter and the branches 10-20 mm. in height by 5-6 mm. in diameter. The substance is hard and calcareous, and the surface is perforated by numerous small pores of various sizes. These pores are clearly not of two categories, large and small as in *Millepora*, but vary from a minimum diameter of .05 mm. to a maximum of .3 mm.² When seen in vertical section these pores are found to pass down into

¹ *Campagnes scientifiques du Prince de Monaco*, fasc. xxiii., 1903.

² These measurements are taken from a specimen of *H. pelliculata* from New Zealand.

long tubes running more or less parallel with one another into the depths of the branches.

Heteropora has been regarded as the last survivor of a group of fossil Polyzoa called the Treposomata, which occur abundantly in certain Palaeozoic rocks and had some representatives in Jurassic times. It has also been described as a Tabulate coral, but the fact seems to be that in some specimens the tubes are divided into compartments by thin calcareous tabulae and in others they are not. The first of the recent specimens were found in the shallow waters of New Zealand, and the genus has more recently been discovered off the coast of South Africa and off the Pacific coast of North America. An examination of specimens from these three localities has shown that in all general characters they are very similar to one another, and perhaps represent only one widely distributed species which should be called *Heteropora pelliculata*.¹ But although a few widely separated tabulae were found by the author in specimens from New Zealand, no trace of such structures were found in the South African and Pacific coast specimens.

CHEILOSTOMATA.—In the Cheilostomata the colony usually consists of a number of cubical oval or oblong chambers (the zooecia) provided with a semicircular or crescentic or sometimes circular orifice protected by a chitinous lip or operculum, a second aperture situated just behind the other in some cases, and numerous minute pores arranged in various ways (see Fig. 78). The general effect produced by this structure of the Cheilostomata when a colony is examined with a lens, is to give the impression that it is composed of a large number of closely fitting cells (Fig. 80), and it is this cellular appearance under a low power which may be taken as the first rough guide to the determination of a coral as a Cheilostomatous Polyzoan.

The only other coral with which it could possibly be confused might be one of the large Foraminifera such as *Gypsina*; but from that it can at once be distinguished

¹ *Heteropora magna*, O'Donoghue, from Victoria, B.C., 8-18 fathoms, may be a distinct species, but *H. pelliculata* also occurs in the same locality (*Contributions to Canadian Biology*, N.S., vol. i., 1923, p. 156).

by the presence of the large orifice for the protrusion of the Polyzoan polyp.

RETEPORA.—One of the commonest objects in a museum collection of Polyzoa is the beautiful little coral frequently called " Neptune's basket " (Manchette de Neptune, Tournef) (Fig. 77).

Its most characteristic form is that of a shallow bowl, from one to two or three inches in diameter, attached by a short round stalk to a shell or stone. The bowl is perforated throughout by numerous round holes or fenestra about 0.75 mm. in diameter, situated at regular intervals apart so that it has the appearance of a net or basket, and was in consequence given the name Retepora by Imperato in 1599. Later observers, noticing that the upper surface of the coral exhibited a large number of minute pores, classified it with many other corals under the general name *Millepora*, and thus it became the *Millepora cellulosa* of Linnaeus.

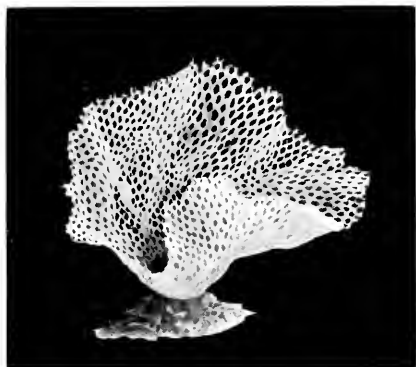


FIG. 77.—Retepora. Nat. size.

The genus Retepora has a wide geographical distribution, being commonly found in the temperate seas, in the Mediterranean, and in the Tropics. There are two British species, both found in deep water: *R. beaniana* occurring off the coast of Northumberland and Scotland, *R. couchii* in the Channel Islands and off the coast of Cornwall.

The colour of the coral is usually white, but in some localities (Torres Straits, Bass Straits, etc.) pink or salmon-coloured specimens are not uncommonly found. The bowl shape of the colony, which is by far the most characteristic form, is in some specimens replaced by a more irregular manner of growth leading up to forms that may be called foliaceous; but in these varieties the characteristic features

of the corallum and even the size of the perforations remain remarkably constant. It is one of the easiest corals to recognise and name.

ADEONA.—Specimens of the exotic genus *Adeona*, found in shallow water off the coast of Australia, Africa, and in the South Seas, attain to the largest size of any of the coral-forming Polyzoa. They consist of thick erect fronds attached by a short flexible stalk to rocks, and they are perforated by a number of round fenestra larger and more scattered than in *Retepora*.

Some very large fronds of this genus, measuring two feet

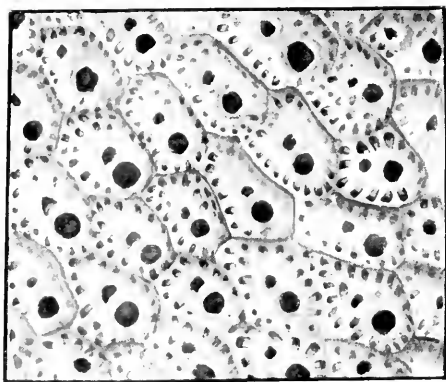


FIG. 78.—*Adeona*. Surface view of a part of a colony. 20 diams.

in height and nearly as much in diameter, have been found, and, as their substance is hard, calcareous, and of considerable thickness, they possess a thoroughly coral-like aspect.

At first sight *Adeona* might be considered to be a large coarse species of *Retepora*, but a detailed examination of the zooecia shows that

it is only remotely related to that genus. Among other points of difference that may be observed is the presence in *Adeona* of a second large aperture situated a little distance behind the orifice and frequently connected with it by a shallow groove (Fig. 78). This second aperture is smaller than the main aperture but distinctly larger than the pores which decorate the sides of the zooecia.

Closely related to *Adeona* is the genus *Adeonella*, which forms masses of variously branched or ramified coral substance sometimes attaining considerable dimensions. The stem in this genus is not flexible as in *Adeona*, but the colony is usually attached to some flexible support.

LEPRALIA.—In dredging in a few fathoms of water off the British coast, the naturalist sometimes finds his net held up or checked by large masses of a foliaceous coralline substance which proves to be a Cheilostomatous Polyzoon belonging to the genus *Lepralia* (*L. foliacea*). The first record of this species seems to be that of Ellis, who wrote: "This stony *Millepora* was found growing to an oyster shell on the west coast of the Isle of Wight in April 1753, and when it was received the Insects were visible in the cells but dead." He called it the "Stony foliaceous coralline" or *Eschara retiformis*.

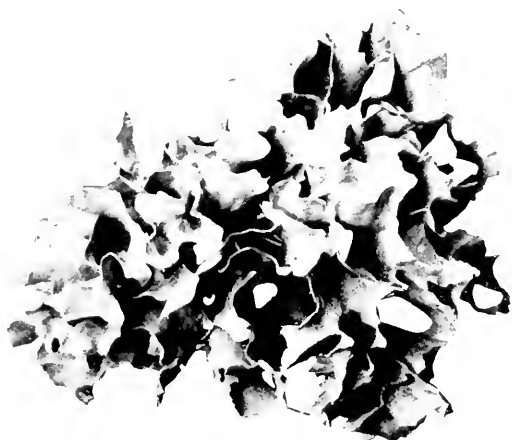


FIG. 79.—*Lepralia foliacea*. From Plymouth. $\frac{1}{4}$ nat. size. Photo by H. Britten.

The specimen which was photographed for the illustration (Fig. 79) was taken off the Mewstone Rock near Plymouth in 1923 in about 12 fathoms of water, and occupied a space of about one cubic foot, but larger specimens than this are not uncommonly found off the coast of Cornwall.¹

When a piece of one of the thin and very brittle laminae or leaves of the coral is broken off and dried, the surface on both sides is seen to be composed of typical Polyzoan zooecia

¹ Couch mentions that he had seen one hooked up by a fisherman off the Eddystone which measured 7 feet 4 inches in circumference and 1 foot in depth (Hincks, *British Marine Polyzoa*, p. 304).

arranged in rows (Fig. 80), and the student of zoology will recognise a close similarity between these zooecia and those of the common sea-mat, *Flustra*. One of the most important differences between *Lepralia* and *Flustra* is that, whereas in the former the walls of the zooecia are impregnated with calcareous matter, in the latter they remain horny in texture. From this difference it follows that in *Lepralia* the fronds are rigid and brittle, whereas in *Flustra* they are flexible and tough.

CELLEPORA.—The genus *Cellepora* includes some species which form, in tropical waters, large spherical, oval, or

irregularly shaped masses of coral substance (Fig. 81); but as the walls of the zooecia are relatively thin the texture of these masses might be called spongy, and they feel light in the hand as compared with other corals.

In these tropical species the lumps of *Cellepora* are frequently invaded by other organisms which seem to live and thrive without material inconvenience to their host.

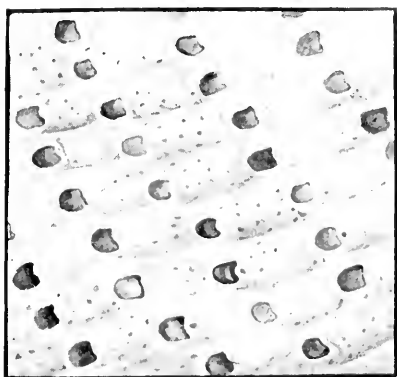


FIG. 80.—*Lepralia foliacea*. Surface view of a part of a colony. 10 diams.

In one ramified specimen from shallow water off the Aru Islands the surface is perforated by little round holes, situated at approximately equal distances apart, in which were living sea anemones. In other specimens barnacles and worm tubes are found.

When these lumps of *Cellepora* are cut across it is generally found that there is a core or kernel of some foreign substance, such as a stone, another coral, or a branching Gorgonian, upon which the Polyzoon has built up layer upon layer of zooecia until the original support is entirely submerged. The final shape of the lump is due in large measure to the shape of the foreign substance on which it started to form its colony.

Cellepora is not the only genus in which these lumps of coral of irregular shape are formed by the overgrowth of successive laminae of zooecia. Lumps of Polyzoa 3 or 4 inches in diameter formed by the zooecia of the genera Microporella and Schizoporella are not infrequently found.

These can be distinguished roughly from the more abundant Cellepora by the smaller size of the zooecia.

It is difficult to give, without going into detailed account

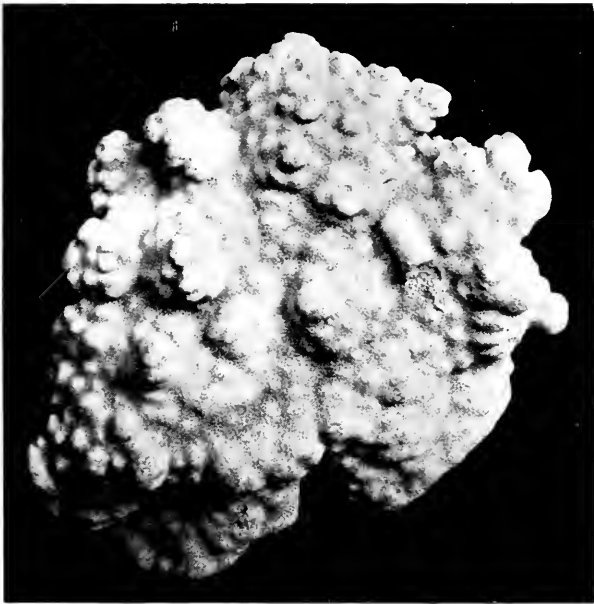


FIG. 81.—Cellepora. From off Auckland, New Zealand. Nat. size.

of Polyzoan structure, the precise characters by which these genera are distinguished from one another by the special workers in this group, but as Cellepora is such a widespread genus it may be of interest to state the characters which serve as a guide to its recognition.

The zooecia of Cellepora are described as flagon-shaped (urceolate) and erect, the end of the zoecium which bears the orifice projecting from the surface, while the base is more or less submerged. The size of the zooecia varies a

good deal, but as a rough guide for comparison with other species, it may be said that the average length of a zooecium is about 0.3 mm.

The zooecia appear to be irregularly disposed with a tendency to overlap and form layer upon layer of superimposed laminae. The walls of the superficial zooecia are very thin and brittle, and there does not seem to be the same tendency for the walls of the lower layers to become thicker, so that the colony as a whole retains its light spongy texture.

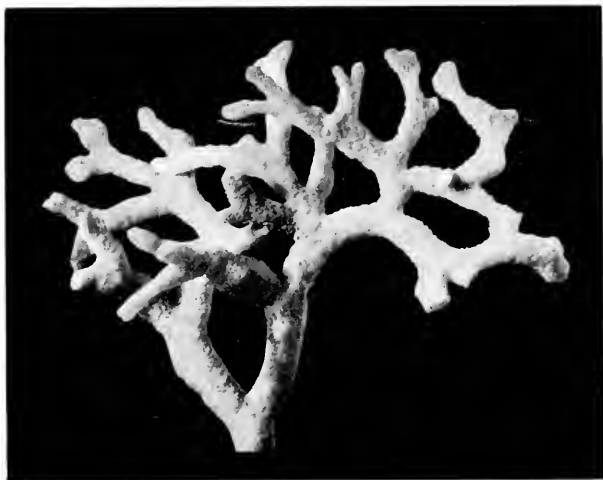


FIG. 82.—*Porella compressa*. From west coast of Scotland. Nat. size.

The genus *Cellepora* includes a very large number of species and several of them are represented in British waters.

One of these, *C. pumicosa*, is very commonly found attached to the seaweed and zoophytes cast up on the beach after a storm. It has the form of little white, or if fresh, pink dome-shaped encrusting masses of zooecia a quarter of an inch or less in diameter.

PORELLA.—This cosmopolitan genus of Polyzoa includes a species of coral, *P. compressa*, which is not uncommonly brought up in the dredge off the coast of Cornwall, off the west coasts of Ireland and Scotland, and in some other British localities. It seems to be confined to deep water

(i.e. 30-200 fathoms). The colony is three or four inches in height and is profusely branched more or less in one plane, the branches freely anastomosing. The terminal branches are usually flattened or compressed and terminate in blunt points, or where they are about to bifurcate, in broad heart-shaped expansions (Fig. 82).

The main stem and the thicker branches are cylindrical, and the calcareous substance of which they are composed appears to be much harder and more compact than the stems of other calcareous Polyzoa, but a close examination of their structure in transverse section shows that they are built up of concentric rings of zooecia with thickened walls. At the surface the zooecia are seen to be largely submerged, but the orifice of each one is raised on a short conical projection and this gives a rough file-like texture to the branches (Fig. 83). On the flat terminal branches the surface is smoother, and as the walls are thinner the complete outline of the zooecia can be more clearly seen.

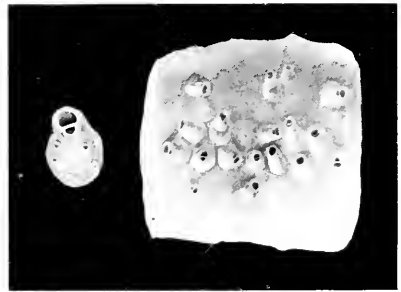


FIG. 83. — *Porella compressa*. Surface view. On the right a part of a branch showing the zooecia 8 diams. On the left a single zooecium 20 diams.

Porella is a very large genus, and among the many species a great variety of form of growth is observed. Some species are erect and ramified like *Porella compressa*, others are flat and encrusting, forming large circular patches on rocks and stones such as the common British shallow-water species *P. concinna*.

The genus *SMITTIA* is closely allied to *Porella* in the structure of the zooecia and some species reach a considerable size. *S. landsborovii*, for example, which occurs in British seas, has a foliaceous variety which might be mistaken for a small specimen of *Lepralia foliacea*, but it can be distinguished from the species by the presence of a small tooth-like projection on the lower lip of the orifice of the zooecium.

CELLARIA.—The genus *Cellaria* (Fig. 84) must be briefly referred to, partly because it includes a very common and widespread species and partly because it affords us another example of a jointed colony, calcareous internodes being connected together by tubular horny nodes.

Cellaria fistulosa is one of the commonest of the British corallines, extending from shallow to deep water in many localities off our own coast, but has also been recorded in the Indian Ocean, off New Zealand, Australia, the Cape of Good Hope, and other distant places, so that it may be regarded as a cosmopolitan species.

It forms typical little coralline tufts or shrubs some two or three inches in height, attached to rocks or shells, consisting of numerous cylindrical and jointed branches dividing dichotomously at the nodes. The internodes are calcareous and are formed by a large number of zooecia arranged usually in longitudinal rows. They are, of course, very variable in size, but in a typical specimen, say from the Firth of



FIG. 84.—*Cellaria fistulosa*. Firth of Clyde. The specimen on the left drawn to nat. size.

Clyde, the internodes may be found to have a length of 10 mm. and a diameter of 0.5 mm. The horny nodes are very short, 0.1 mm. in length, but quite sufficient to give the colony the necessary flexibility to yield without breaking to the movement of tides and currents.

In the description that has been given in the preceding pages of a few representative genera of calcareous Polyzoa, some idea may be gained of the range of form and structure of coralline skeleton found in this group. It may also serve

to assist the collector to distinguish the Polyzoa from other corals. But the scope of the present work does not permit any attempt to be made to give such a detailed account of the very large number of genera which are included in the group as will enable him to identify his specimens and give them the correct names they should bear in his collection. Both the Orders of calcareous Polyzoa, but particularly the Cheilostomata, present many difficulties for the systematist. Like many other animals that lead a sedentary life and form plant-like colonies by the rapid asexual reproduction of the polyps, there is a very wide range of variation in the general form and in some of the details of structure, so that there is some difficulty in drawing the boundary lines between closely related genera and species. It is necessary, therefore, for the naturalist to consult the special memoirs on the group¹ if he wishes to get the correct names for his specimens.

From the frequent references that have been made to the occurrence of calcareous Polyzoa off the British coasts it may be inferred that this group of corals is well represented in the waters of the temperate regions of the world. It is not necessary for the naturalist to visit the coral reefs of the Tropics if he wishes to find abundant material for their study. He will be able to discover as rich a fauna of this description in European waters as anywhere else.

The warmer tropical waters of the world might seem to be less favourable for the growth of Polyzoa, because these relatively small corals are apt to be lost sight of among the bewildering complex of huge and fantastic zoophytes of other Orders that are crowded together in every locality of the sea-bottom that is suitable for the growth of corals. But it has been shown that when the marine fauna of tropical waters is carefully and critically examined a great abundance and a great variety of calcareous Polyzoa can be found. It is probably not a fact that tropical water is unfavourable

¹ T. Hincks, *History of the British Marine Polyzoa*, 1880; G. R. Vine, *Report on Recent Marine Polyzoa: Reports of British Association Meeting at Aberdeen*, 1885, vol. iv. References to more recent memoirs and treatises will be found in the works of Jullien and Calvet; *Campagnes scientifiques du Prince de Monaco*, fasc. xxiii., 1903, and S. F. Harmer, *Reports of Siboga Expedition*, livr. lxxxv., 1915.

to the life of these creatures, but that it is so favourable to the growth of others of similar habits that they seem to be lost in the crowd.

Two examples of large numbers of a calcareous Polyzoon occurring in a tropical locality which have attracted the attention of the author of this volume in recent years, may be referred to in order to emphasise the point that such localities are not necessarily unfavourable for the study of the group.

LAGENIPORA.—In a sample obtained by Mr. Townsend of a shelly sea-bottom from a depth of 156 fathoms at the mouth of the Persian Gulf, large numbers of specimens of a Cheilostomatous Polyzoon were found which belong apparently to the genus *Lagenipora*. They consist of little dome-shaped colonies about 5 mm. in diameter formed by 50-100 flask-shaped zooecia arranged radially from the centre (Fig. 85).

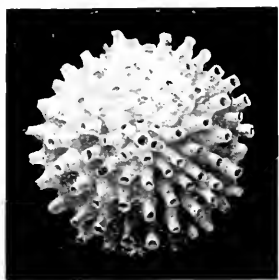


FIG. 85.—*Lagenipora*. From the Persian Gulf, 156 fathoms. · 10 diams.

There are two curious points for consideration about the occurrence of *Lagenipora* in this spot. In the first place the genus has hitherto been found only in the glacial Arctic region and on the British coast. It seems strange, therefore, that it should be discovered in a locality where the surface waters are probably as hot as they are anywhere in the world and at such a long distance from their other habitats. In the present state of our knowledge it might be premature to say that this is a case of discontinuous distribution, but it is, at least, an interesting example of many that are found in the same group of a wide geographical distribution of a genus. In the second place, all the specimens are free. There is no evidence to be found of any basal plate of attachment or of any supporting substance, and none of the great variety of shells with which it was found were suitable in character to give them a permanent upright position.

All the specimens show signs of being more or less water-worn, and it is probable, therefore, that they do not live in the spot where they were found but have been carried there from some other locality by the sea currents. When this locality is discovered and complete living specimens have been examined, some of the problems that have arisen from the discovery of these interesting corals will perhaps be solved.

HASWELLIA.—The other example was found in a collection of Alcyonaria made by Professor Haddon from shallow



FIG. 86.—Haswellia. From Torres Straits. A part of a terminal branch.
× 10 diams.

water in the Torres Straits. Attached to the Alcyonaria the author found large numbers of a delicate branching coralline Polyzoan belonging to the genus *Haswellia* (Fig. 86). The most characteristic feature of this genus is that the zooecia are arranged in more or less regular whorls of five or six and are cylindrical in shape, and in the older branches almost completely submerged. The verticillate arrangement is indicated by the rings of short collar-like tubes on which the main aperture of the zooecia is mounted. In the specimens from the Torres Straits the largest complete colonies are about two inches in height and the branches are about $\frac{1}{25}$ inch (1 mm.) in diameter.

CHAPTER IX

FORAMINIFERAN AND SOME OTHER CORALS

“ J’ai bien constaté que toutes les loges sont occupées à la fois par la substance glutineuse ; mais je n’ai point vu les expansions, non plus que dans le *Polytrema*, que je conjecture appartenir à cette même famille (les Infusoires) d’après la nature de la partie vivante.” —DUJARDIN, *Suites à Buffon : Infusoires*, p. 259.

THE Foraminifera are best known to naturalists as the constructors of the minute flask-shaped, oval, or chambered shells that are found, sometimes in immense numbers, on certain sands of the sea-shore or in the mud of the abysmal depths of the ocean, and it might seem to many that it would be quite out of place to include any of them in a treatise on Corals. And yet there are some calcareous structures formed undoubtedly by these primitive protoplasmic organisms which have been classified with other corals in the past history of zoology, and to this day might very readily be regarded as the production of some Coelenterate or Polyzoan organisms unless carefully examined.

It is true that the vast majority of Foraminifera are free and carry their calcareous skeletal structures with them as they slowly creep along on the seaweed or drift at the surface of the sea, and to such structures the word “ shell ” of our common language is correctly applied. But when, as in the cases to be described in this chapter, the calcareous structure is permanently fixed to a foreign substance, which may be a stone or a rock or a piece of seaweed, and grows and branches into a tree-like form or constructs layer upon layer of calcareous chambers to form a thick crust upon its support, the word “ shell ” is not appropriate. The only

common word in our language which really conveys the correct idea of their general form and structure is the word "coral."

Many of the multilocular shells of the Foraminifera have a spiral form similar to the shell of the pearly Nautilus and some of its fossil relatives, and it was this resemblance in form which led D'Orbigny into the error of supposing that the Foraminifera were microscopic Cephalopods. The discovery of the protoplasmic consistency of the body and of the delicate network of pseudopodia they emit was made by Dujardin, who definitely and correctly placed them in the division Rhizopoda of the great group of unicellular animals called the Protozoa.

POLYTREMA.—The most familiar and probably the most abundant of all the Foraminiferan corals is *Polytrema*. It has usually the form of a short branching coral-like structure 4-5 mm. in height attached by a flat and sometimes spreading base to a foreign body. It has generally a pink or carmine-red colour, but white varieties have been found in many localities. It has a wide distribution in the warm and tropical waters of the Old World and Pacific Ocean, but, strange to say, is very rare in the West Indies and tropical waters of the Eastern American coasts. It is extremely abundant in the Mediterranean Sea, being found attached to corals, zoophytes, to the leaves of *Zostera*, and to Algae of various kinds. In some places broken, water-worn, but sometimes remarkably perfect specimens form an important constituent of the sands cast up on the shore. Among the most remarkable of these sands are the "sables rouges" near Ajaccio off the coast of Corsica, which owe their red colour to the vast numbers of whole or fragmentary specimens of *Polytrema*. It was in these sands that Mr. Heron-Allen discovered the rich material for his description, to which reference will presently be made, of the important stages in their life-history before and after fixation to a foreign substance.

The first description of *Polytrema* is that given by Pallas in 1766, who classified it with that heterogeneous medley of corals called *Millepora* by the older writers. It had previously been seen by Tournefort (1700), who made

the grievous blunder of supposing it to be the young stage of the true Red coral (*Corallium nobile*) ; but it was the distinguished French naturalist Dujardin who, having observed in 1841 a "substance glutineuse" in the chambers, placed it tentatively among the Rhizopoda.

The genus has since been thoroughly investigated by Möbius, Merkel, and other investigators, and its place in the group of the Foraminifera has been firmly established.

It is not necessary to describe in detail the structure and life-history of the organisms that form the shells and corals of the Foraminifera, but it may be said that by no extension of the meaning of the words can they be called "polyps" or "zooids." They consist of a mass of the granular semi-fluid living substance called Protoplasm and show no differentiation into cells and no structural organs. There are no tentacles, no mouth, and no defined digestive canal or cavity. Embedded in the substance of the protoplasm there is a nucleus or, in some stages of the life-history, several nuclei.

The food of the *Polytrema* is obtained by a network of very delicate but anastomosing protoplasmic filaments which project from the ends of the branches. These filaments are called the Pseudopodia.

When the dried calcareous structure of the *Polytrema* (Fig. 87) is examined carefully with a lens, the surface of the base and of the branches is seen to be perforated by a number of minute holes. There are two kinds of holes, the larger kind called the "pillar pores" and the far more numerous smaller kind called the "foramina" (Fig. 88, A). The substance of the coral below the surface is built up by the perforated calcareous walls of a number of chambers which are arranged more or less concentrically at the base, but are much more irregular in the stem and branches. Moreover, in the axis of the stem and branches there is a tendency for the cavities of the chambers to fuse so as to form an irregular but continuous lumen, the branches thus becoming hollow or tubular.

This lumen ends at the extremity of each of the branches in a large irregularly round aperture, and projecting from the

lips of this aperture there may be seen in well-preserved specimens a number of needle-like spicules. The presence of these spicules carefully arranged in this position to act as scaffolding poles for the support of the new chambers as they are formed has given rise to some controversy. They are not composed of the same chemical substance (calcium carbonate) as the walls of the chambers and are not soluble in weak acids, and it is generally supposed that they are the siliceous spicules of some sponges which the pseudopodia have collected from the surrounding medium and placed in this position.

The habit of collecting the spicules of sponges, grains of sand, and other foreign bodies, and incorporating them in the skeletal structures is found in many other genera of Foraminifera, so that in this respect *Polytrema* is not peculiar; but there are many interesting questions that



FIG. 87.—*Polytrema miniaccum*. A branching specimen attached to a piece of *Ramulina*. The fragile ends of the branches are broken off, showing the chambers. $\times 3$ diams.

arise about this habit which require further careful investigation. It is, for example, very difficult to understand how the *Polytrema* can find the required spicules in some localities, how they can select spicules of the proper length and kind, and how they are dissolved at a later period when the calcareous secretions have surrounded them in the construction of the chambers.

As a final word in this very brief account of the structure of *Polytrema* it should be said that the calcareous skeleton is extremely brittle. The stem and branches can be easily crushed between the finger and thumb. This is in striking contrast to the next two genera to be described in this chapter, which are more solidly built.

There are still some gaps to be filled up in our knowledge of the life-history of *Polytrema*, but it is known that before the young *Polytrema* becomes fixed to its support it lives a free life like the majority of the Foraminifera and possesses a shell of three or four chambers which has a close resemblance to the shells of the genus *Rotalia*. This stage is known as the "rotaliform young." At a subsequent stage, when successive chambers have been formed around the primary ones, it assumes a roughly globular form like a raspberry, and if this stage continues and it becomes more irregular it assumes a form like that of some species of

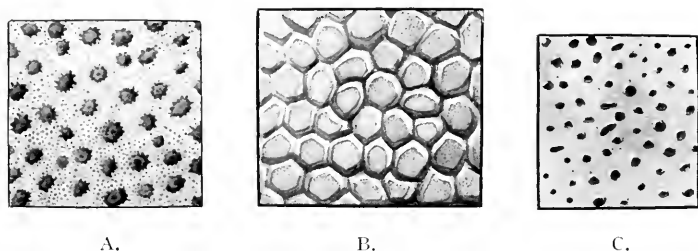


FIG. 88.—Surface views of A, *Polytrema*; B, *Homotrema*; C, *Sporadotrema*.
 · about 20 diams.

Gypsina. If the *Gypsina*-like form finds a suitable object it becomes attached to it and constructs an irregular thin plate of chambers, connecting it with its host, which subsequently increases in thickness and submerges the primary chambers. At a later stage the beginning of the stem is seen arising as a dome in the centre of the upper surface.¹

The account that has been given of the general form of the full-grown *Polytrema* applies to specimens which have been able to develop freely in comparatively quiet waters or sheltered places. But the coral is so brittle that the stem and branches are very liable to be broken off in their natural habitat in the sea, or more particularly in the process of collecting and the subsequent handling of the specimens. It thus comes about that the most familiar form of *Polytrema* is not the branching form but that of little pink

¹ For a full account of this development see Heron-Allen and Earland, *Zoology of the "Terra Nova" Expedition*, vol. vi. No. 2, 1922, p. 222.

encrusting discs on corals or shells, which may or may not show the scars of the broken-off stems. Specimens of this kind can frequently be found on the dead branches of other corals or on shells from tropical waters of the Indian and Pacific Oceans.

HOMOTREMA.—Until quite recently the genus *Homotrema* has been confused with *Polytrema* on account of its size, colour, and habit, but a detailed study of its structure proves that the two genera are quite distinct.

If corals and shells from the reefs of the West Indies be examined they will frequently be found to bear little red spots and discs very similar to the spots and discs of *Polytrema* found on corals and shells from the Mediterranean Sea and the East Indies, and some of them may support short knobbed processes something like a minute pollarded willow tree (Fig. 89).

Pallas seems to have noticed two of the characters which distinguish *Homotrema* from *Polytrema*, for he says that the specimens from American seas are of a darker red colour than those from the Mediterranean Sea, and that they have the form of large irregular warts from the surface of which a few short branches spring.¹ But Pallas did not feel justified in separating the two varieties, and included them both in his species *Millepora miniacea*.



FIG. 89.—*Homotrema rubrum*. $\times 2$ diams.

The characters that separate *Homotrema* from *Polytrema* may be summarised as follows: The form may be that of a simple encrusting disc, but, when standing erect from a spreading base, of the shape of a wart or knob with sometimes a few very short projections at the free extremity. The surface is mapped out into areas which are slightly

¹ "Color hujus elegantissimi Corallioli ex mari Mediterraneo allati, pallide roseus esse solet, interdum saturator. Quod in coralliis Indicis reperitur pulchre cinnabarinum colorem exhibet; saturatissimum vero specimina in Coralliis testisque exesis Maris Americani reperiunda. Americana varietas plerumque verrucae magnae inequalis speciem habet, quae superficie sparsos ramulos exserit."—Pallas, *Elenchus Zoophytorum*, 1766.

convex and perforated by minute foramina surrounded by solid imperforate boundaries (Fig. 88, B). There are no pillar pores. The colour is almost invariably of the dark red tint which is technically known as salmon colour. No white varieties have been found. In addition to these characters, which can be observed without dissection, there are other characters of the internal chambers which separate the genus clearly and distinctly from *Polytrema*.

The most curious fact about the two genera is perhaps that of their geographical distribution. A very large number of dried corals and shells from various islands of the West Indies and the Western American coasts have been examined, and without exception the red foraminiferan discs attached to them have invariably shown the *Homotrema* characters.¹

In the Mediterranean Sea *Polytrema* is very abundant, and *Homotrema* does not occur. In the tropical Indian and Pacific Oceans both genera occur, and sometimes specimens of the two are found on the same piece of coral, but on the whole *Polytrema* is the more common. In the New Zealand area *Polytrema* was found by the *Terra Nova* expedition to be abundant, but no specimens of *Homotrema* were obtained.

No specimens of either genus have been found either in the Arctic or Antarctic Seas.

SPORADOTREMA.—The third genus of this series of Foraminifera is *Sporadotrema*, which more fully justifies its place in a book on corals in being larger and more robust than the other two.

The first specimens of this genus to be discovered were found by Captain Warren in the Gulf of Manaar and were described by Carter under the name *Polytrema cylindricum*; but the richest collection of specimens was made by Stanley Gardiner, dredging in water 30-150 fathoms in depth in the Indian Ocean.²

Specimens have also been found in Torres Straits, off the Philippine Islands, and in the tropical Pacific Ocean. The

¹ Since the above sentence was written one specimen of *Polytrema* from Barbadoes has been found.

² S. J. Hickson, *Transactions of the Linnean Society of London*, vol. 14, 1911.

genus is not known to occur in the Mediterranean Sea or in the West Indies.

In the case of *Polytrema* and *Homotrema* the specimens from various parts of the world are so much alike, both in form and minute structure, that it is reasonable to suppose there is only one species of each genus; but in the case of *Sporadotrema* it is necessary to divide the genus into two species, *S. cylindricum* and *S. mesentericum*.

The form of *Sporadotrema cylindricum* is always erect, a thick solid stem springing from a restricted base and giving rise to a few thick branches (Fig. 90). No flat disc-shaped encrusting specimens have yet been found. The surface of the stem and the proximal parts of the branches are perforated by a number of foramina of relatively large but variable size and irregularly scattered. There are no areolae and no pores (Fig. 88, C). In some specimens, the chambers of which the corals are composed (Fig. 91) are indicated on the surface at the ends of the branches by a number of convex areas perforated by relatively large foramina.



FIG. 90.—*Sporadotrema cylindricum* from Providence Island, Indian Ocean, 70 fathoms. $\times 2$ diams.



FIG. 91.—*Sporadotrema cylindricum*. Photograph of a section through a specimen showing the chambers and the thick outer wall perforated by the foramina. $\times 5$ diams.

Another very striking character of the species is the colour variety. Some specimens are dark purplish red, others pink, yellow, or orange coloured.

Large specimens are over an inch in height and in expanse, and many specimens just under an inch both ways are to be found in the collections. Although size is not as a rule an

important character in the determination of corals, it is so in this case, because the two genera with which *Sporadotrema cylindricum* is most likely to be confused never exceed a quarter of an inch in height.

It may have been thought at one time that *Sporadotrema cylindricum* was only a robust and overgrown variety of *Polytrema*, but there is no foundation for this belief. The two genera are quite distinct. Apart from important differences of detail in the structure of full-grown examples of the two genera which it is not necessary to describe in this place, the young immature stages are as distinct as the adults. A young *Sporadotrema* growing on the same support as a

larger specimen of *Polytrema* exhibits all the important characters of its genus and could not be mistaken for a young specimen of either of the other two genera.



FIG. 92.—*Sporadotrema mesentericum* from Torres Straits. $\times 2$ diams.

Sporadotrema mesentericum (Fig. 92) appears to have a much more restricted range than that of *S. cylindricum*, having been found only in shallow water in Torres Straits.

The form of this species is characteristic, as it consists of a number of more or less erect sinuous laminae arising from a spreading encrusting base. The margin is thick and crenate. The laminae are sometimes interlaced so as to form a kind of labyrinth of laminae, but in the simple condition of a single lamina the form has a rough resemblance to a cock's comb. In full-grown specimens the laminae are 15-20 mm. in length, from 7 to 8 mm. in height, and from 1.5 to 2 mm. in thickness.

All the known specimens are of a salmon-red colour. As regards the surface characters and general structure the species does not differ in any material respects from *S. cylindricum*, and it clearly belongs to the same genus.

GYPSINA.—The genus *Gypsina* (Fig. 93) is a Foraminifer which, like many others, sometimes becomes attached to some rock or shell and forms encrusting discs or laminae ;

but the great majority of these encrusting Foraminifera do not attain to a size of more than a millimetre or two in diameter and need not, therefore, be referred to in detail. There is, however, a variety of *Gypsina plana* which reaches

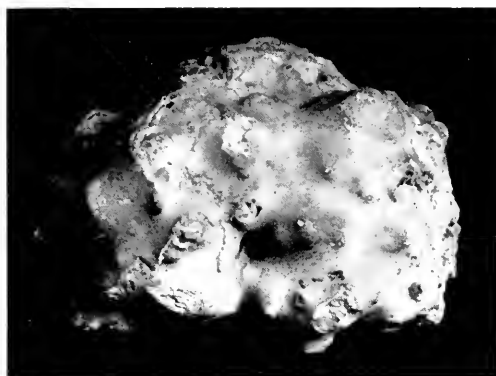


FIG. 93.—Gypsina. *Gypsina plana*. From Mauritius, 100 fathoms. Nat. size.

such a gigantic size—for a Foraminifer—that it might well be mistaken for a coral of another Order.

Like other Foraminifera the substance of *Gypsina plana* is built up of minute chambers with walls perforated by the foramina, and when the young free form becomes adherent to a stone the chambers increase in numbers at the circumference and by the formation of laminae after laminae of new chambers growing over the surface of the old ones (Fig. 94). In some specimens obtained by Prof. Stanley Gardiner in deep water (25-100 fathoms) in the Indian Ocean these laminated masses of *Gypsina* have formed a thick crust entirely surrounding their original support, and have the appearance

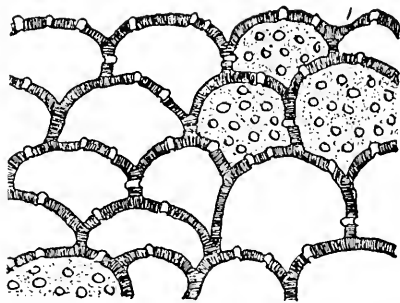


FIG. 94.—Vertical section of *Gypsina plana* showing the perforated chambers. From a drawing by Miss Lindsey. $\times 120$ diams.

of lumps of water-worn coral reaching a size of 3-4 inches in diameter.

The general appearance of these large encrusting forms of *Gypsina* is much like that of some other corals of a similar habit described in this book, and the occurrence of Foraminifers of this size is so extremely rare that it would not be surprising if a collector of corals in general were to make a mistake in classifying them. A few notes may therefore be written to describe the principal characters by which they can be recognised as Foraminifera.

The surface of the coral when magnified exhibits a number of closely fitting and slightly convex areolae varying in size from 70 to 230 microns (*i.e.* .07-.23 mm.). These areolae representing the outer walls of the chambers of the superficial lamina are perforated by numerous foramina. They might be thought to be the walls of the zooecia of a calcareous Polyzoan, but they differ from them in the absence of the large aperture or orifice for the protrusion of the Polyzoan polyp.

The only other kind of coral for which they might be mistaken would be the calcareous algae, but the surfaces of the calcareous algae have either no areolae (cf. *Halimeda*, p. 210), or if they show in some places convex areolae (cf. Fig. 101, facing p. 201), these areolae are not pierced by more than one foramen.

There is one more point of interest about these large specimens of *Gypsina plana*. They are so much bigger than the specimens of *Gypsina* (not exceeding 1-2 mm. in diameter) with which the student of the Foraminifera is most familiar, that it may seem remarkable that they have not been relegated to a distinct genus.

Fortunately, however, it has been possible to examine¹ a large number of specimens from the smallest to the largest, and it has been found that not only is there a fairly complete series as regards the size of the specimens (1-100 mm.), but also as regards the size of the constituent chambers (20-230 microns).

¹ M. Lindsey, *Transactions of the Linnean Society of London*, vol. 16, 1913.

RAMULINA.—One of the most remarkable results of the recent oceanographic investigations has been the revelation of the extraordinary variation of the constitution of the sea-bottom in areas situated a few miles from the coast-line. There are various designations given to express the nature of these deposits, all of them more or less vague and indeterminate—such as “mud,” “sand,” “shell,” “gravel,” “rock,” and “coral.” In the hope of giving some assistance to those who wish to use a more precise designation to a so-called “coral” sea-bottom deposit, a description is given in this book of various kinds of coral which play an important part in the formation of such deposits in various parts of the world.

One of the most interesting of these is the deposit discovered by Herdman along the 100 fathom line about 12 miles south of Galle in Ceylon. In this locality the dredge brought up masses of a calcareous

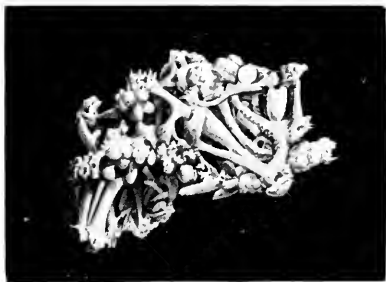


FIG. 95.—*Ramulina herdmani*.
From Ceylon. Nat. size.

structure from $\frac{1}{4}$ to over 2 inches in diameter, which was named by Dakin *Ramulina herdmani*. Unfortunately nothing is known for certain about the living organisms that form these calcareous structures, but there are sufficient reasons for believing that they are Foraminifera.

“They consist of a mass of anastomosing calcareous tubes inextricably commingled and assuming two principal forms of growth. Many specimens show a long series of globular segments, arranged irregularly, and opening directly into one another by large openings. These globular chambers at intervals give off numerous radiating straight tubes varying in length from quite small outgrowths to 1.25 centimetres with a diameter of 1.5 mm. to 2 mm. These straight portions may run in the same direction, separating but little and becoming compact, or they may diverge and radiate from a common centre. Eventually they reach either the

globular chambers or other straight tubes with which they fuse, the cavities becoming continuous" (Figs. 87, p. 179, and 95).

"All the walls are uniformly perforate, but the external surface differs in appearance in places, being sometimes quite smooth and elsewhere bearing minute denticles either sparsely or more closely set. There also seem to be definite larger openings to the exterior."¹

The genus *Ramulina* was founded by Rupert Jones in 1875, and seems to have a world-wide distribution in depths of 50-700 fathoms of water.

PORIFERAN CORALS

MERLIA.—Among the many encrusting calcareous organisms that have for a time puzzled the experts there is no one more interesting and remarkable than *Merlia normani* (Fig. 96).

At first it was thought to be a Polyzoon, then certain characters were discovered which suggested the view that it was a Foraminifer, but it has at last settled down into a position among the Sponges, where it must remain until some unexpected evidence is forthcoming to prove that it has been wrongly classified. The first specimens to be discovered were found in sixty fathoms of water off Porto Santo Island near Madeira. They consisted, when dry, of an encrusting calcareous substance covered by a thin yellow pellicle.

On examining sections of this substance siliceous pin-shaped spicules were found in the upper layers, and consequently it was suggested that the yellow pellicle was the remains of a sponge which had grown over and perhaps smothered the organism that had formed the calcareous substance.

It is well known that in the Order of the Sponges (Porifera) one group of genera forms calcareous spicules and another siliceous spicules, but it was considered to be very unlikely

¹ Dakin, *Reports on Ceylon Pearl Oyster Fisheries*, 1906, v. p. 228.

that any sponge would be found that formed both a siliceous and a calcareous skeleton as well.

We are indebted to Mr. R. Kirkpatrick of the British Museum, who made a special journey to Porto Santo to obtain living specimens of *Merlia*, for a careful investigation and description of fresh material and for the conclusion, which seems to be convincing, that the calcareous substance of *Merlia* is formed by the Sponge.¹

All the specimens of *Merlia* that have hitherto been described were found in deep water off Porto Santo or off the coast of Madeira, but a very fine specimen was obtained by Professor Gardiner off Solomon Island in the Indian Ocean, and it is probable, therefore, that the genus has a wider geographical distribution than was at first supposed.

The living specimens have a smooth surface and are bright vermillion in colour, but when removed from the sea the thin layer of fleshy substance settles down and reveals the porcelain-like calcareous skeleton.

The dried specimens have the appearance of thin crusts of calcareous matter of irregular but roughly circular form about 10-15 mm. in diameter, firmly adherent to some hard support. Unlike many encrusting corals, *Merlia* cannot be detached from its support without being hopelessly destroyed. The character of the support varies. In the Solomon Island specimen it is a mass of porous coral substance so much altered by age and boring organisms that it is impossible to determine its precise nature. The Atlantic specimens were attached to shells, branches of corallines, worm tubes, a dead *Dendrophyllia*, and a block of volcanic rock.

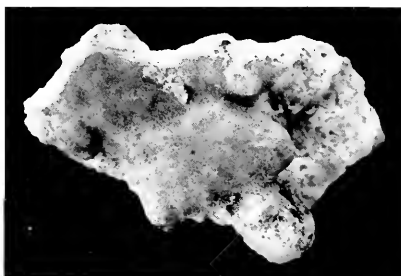


FIG. 96.—*Merlia normani*. Solomon Island, Indian Ocean. Nat. size.

¹ R. Kirkpatrick, *Quart. Journ. Micr. Sci.* lvi., 1911.

When the surface of the coral is examined with a lens it is seen to be perforated by a number of cylindrical tubes, and between these tubes the calcareous walls rise up in polygonal ridges which are ornamented with columella-like tubercles where the angles of adjacent polygons meet (Figs. 97 and 98).

If the specimens are sufficiently well preserved to show these tubercles they present a surface character which is quite sufficient to distinguish *Merlia* from any other coral, but of course this character is the first to disappear if the specimens are water-worn.

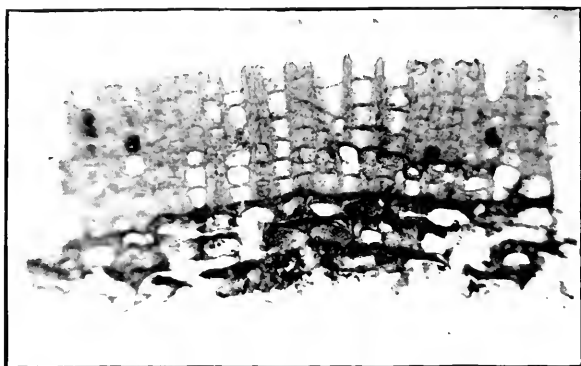


FIG. 97. — *Merlia normani*. Photo of a vertical section through a fragment of a specimen from Solomon Island showing the vertical tabulate tubes of which it is composed. $\times 15$ diams

On examining a vertical section or fractured edge of a specimen the most interesting character is seen in the presence of a series of flat tabulae dividing the cavity of the vertical tubes into a number of chambers or "crypts." *Merlia* is therefore a tabulate coral. The tabulae, however, differ from the usual form of tabulae in the fact that they seem to be always perforated in the centre by a little round hole of communication between two adjacent crypts.

The investigation of fresh material has shown that the sponge which forms this remarkable skeletal structure belongs to the Family Haploscleridae and the Order Monaxonellidae, but its most curious character is that certain

cells which appear to be of the general nature of amoebocytes take upon themselves the function of secreting calcium carbonate (calcocytes), and it is with these remarkable cells that the crypts are filled.

ASTROSCLERA.—Another very remarkable calcareous structure which seems to be undoubtedly the production of a sponge is *Astrosclera willeyana*.¹

The type specimen from Lifu is a little hard calcareous knob about 8 mm. in height by 5 mm. in diameter. The stem is cylindrical and smooth with a spreading base attached to a dead coral; the upper end is convex and scored by an irregular labyrinth of pits and grooves. A specimen from Funafuti is shaped like a short-stalked fungus with a disc 20 mm. in diameter. Other specimens are more irregular in shape, but they all show grooves and pits on the upper free surface.

In a vertical section the interior of the coral is seen to be penetrated by a system of anastomosing channels, many of which have a longitudinal direction and eventually open to the exterior in the pits of the upper surface. In fresh specimens the soft tissues of the sponge cover the distal surface and, extending beyond it some little distance down the stem, penetrate into the anastomosing channels in the corallum.

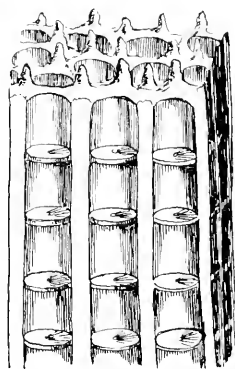


FIG. 98.—Diagram to illustrate the structure of *Merlia*. 40 diam.

Astrosclera has hitherto been found in 35 fathoms of water off Lifu in the Loyalty Islands, and in 100 fathoms off Funafuti in the Ellice group.

PETROSTROMA SCHULZEI.—Another sponge which forms a hard calcareous structure is *Petrostroma schulzei*, found at depths of 100-200 fathoms of water off the coast of Japan. According to Döderlein² it represents a distinct family of calcareous sponges which he calls the *Lithonina*.

¹ J. J. Lister in Willey's *Zool. Results*, Part IV., 1900; and *Cambridge Natural History*, vol. i. p. 194.

² Döderlein, *Zool. Jahrb., Syst. N.*, 1898.

In external form it might be mistaken for a *Millepora* or a *Heteropora*, as it consists of a broad base from which a number of short cylindrical or flattened dichotomously divided branches rise to a height of an inch or more.

When fresh the white coral substance is covered by a white or yellow film of sponge substance and spicules, but this disappears when it is dead and macerated.

The dried coral may be distinguished from other corals by its spongy texture and the absence of any regular pores or channels, but more particularly by the character of the surface, which is provided with a number of small pointed vertical pillars like a palisade. Among these pillars there may be found some of the characteristic forked calcareous spicules which are sufficient by themselves to suggest to the naturalist that the structure must have been formed by a sponge ; but a careful study of the coral with a lens shows that the pillars at the surface and the subjacent structures have been formed by the growth and fusion of these spicules.

ANNELID WORM TUBES

In the examination of corals of various kinds the naturalist frequently finds a number of long, straight, coiled, or twisted calcareous tubes which have been formed by different kinds of Polychaet worms.

In such a tangled mass of coral as that shown in the illustration of *Lophohelia* (Fig. 5, p. 28) a number of such tubes, distinguished by their smooth cylindrical contour and the absence of septa, are invariably present. In *Helio-pora* again the corallum is always perforated by small tubes of the same kind (Fig. 52, p. 119). There are many corals which possess some power of protecting themselves from uninvited guests of this sort, but still it must be said that most corals are liable to be penetrated by and frequently distorted and disturbed in their normal manner of growth by certain kinds of sedentary polychaet worms.

The relation between the hosts and the guests in this association may not be clearly understood. It is difficult to believe that the coral hosts are ever seriously incon-

veniened by the worm guests. They may not grow into exactly the same shapes as they would without them, but they show no signs of reduced vigour or general health. In some cases, such as that of *Heliopora* and *Leucodora* (p. 119), the association appears to be constant, the *Heliopora* always harbouring its *Leucodora* guests, but in others the worms may or may not be present, and the corals without the worms are apparently as healthy as those with them. There is no reason, therefore, to suppose that the worms in any way assist their coral hosts in the struggle for existence. The association must be regarded as one of commensalism, the host and guest feeding at the same table, without injuring or benefiting each other.

It does not seem to be a case of mutualism such as that of *Heteropsammia* (p. 78) and the Sipunculid worm, in which both the host and guest benefit by the association, and more certainly it is not a case of parasitism. The worm must not be branded with the stigma of a parasite.

But although they are so often associated with corals it must be remembered that the tubiculous worms are also found in immense numbers living an independent life attached to various kinds of solid objects. Every one must be familiar with the little spiral tubes of *Spirorbis* attached to the seaweed and stones that are washed up on the beach and the larger meandering tubes of *Serpula* attached to oyster shells. Not infrequently it is found that tubes of *Serpula* will almost completely cover the shells on which they have settled, and sometimes they run over one another in serpentine fashion to form lumps of intertwined calcareous tubes several inches in diameter.

It is perhaps stretching our definition of the word beyond its legitimate boundaries to call such lumps "coral." It would be better if they could always be called "worm tubes."

But there is one of these Polychaet worms which forms great masses composed of a labyrinth of small calcareous tubes that are frequently many inches in diameter and might readily be mistaken for a coral.

The genus *Filograna* (Fig. 99) seems to have an almost world-wide distribution in shallow water, and sometimes is

found in masses as big as a "boy's head" on the Scottish and other coasts of Great Britain. It seems to be fond of situations in which there is a good flow of water, and has been found choking the supply pipes of an aquarium.¹

The mass is built up of an immense number of small branching calcareous tubes about 0.5 mm. in diameter, and is honeycombed with irregular spaces which harbour various kinds of marine creatures (Fig. 100). It is not hard, as coral substances usually are, but delicate and friable, and unless handled with care breaks up into minute fragments.

The appearance of the living colonies of *Filograna* has

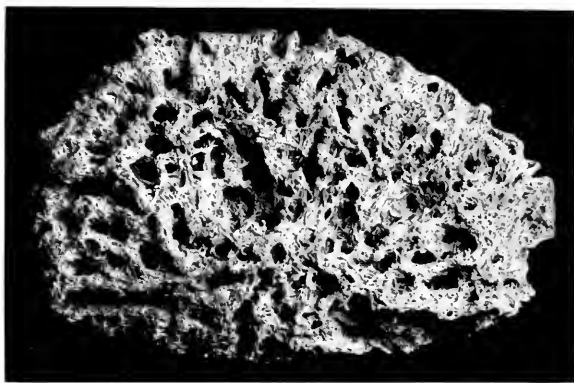


FIG. 99.—*Filograna implexa*. $\frac{1}{2}$ nat. size.

been described by Professor McIntosh² as follows: "Fresh examples from Plymouth in sea-water, as Huxley and others truly said, resemble corals in so far as the branchial fans of the annelids project from the tips of the tubes as miniature flowers, the distal parts (branchiae) of which are pale greenish yellow and the anterior region of a fine reddish hue which tints the cephalic region at the base of the branchiae and passes a short distance along each filament. When eggs are present the posterior region is also reddish, the colour of these being of a brighter hue than the front. Two dark

¹ Prof. McIntosh, "Notes from the Gatty Marine Laboratory, St. Andrews," (xlii.), *Ann. Nat. Hist.* iii., 1919.

² *l.c.* p. 149.

eyes occur on the dorsum of the reddish cephalic area. The anterior (thoracic) membrane is more deeply tinted in front than behind. When in full vigour the pure white of the calcareous tubes, the scarlet of the anterior region which projects beyond them, and the pale greenish yellow fans with their opaque tips make a picture at once beautiful and characteristic."

Reference has already been made to the world-wide distribution of this beautiful and interesting tubicolous

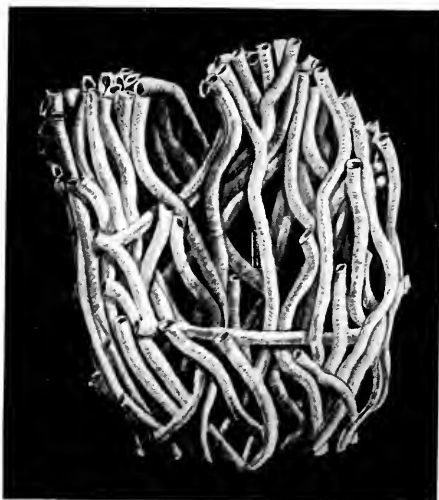
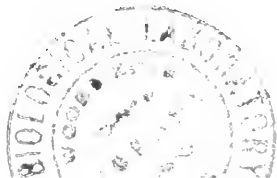


FIG. 100.—*Filograna implexa*. A small part of the mass of serpentine tubes.
× 5 diams.

worm, but to avoid misunderstanding it should be stated that the species and varieties which have been described by various authors under the generic name *Salmacina* are here included in the genus *Filograna*. The only essential difference which was supposed to separate the two genera was the presence of an operculum to close the mouth of the tube in *Filograna* and its absence in *Salmacina*, but McIntosh has shown, in a recent paper, that this character is so variable, even in specimens from the same locality, that it is quite unreliable for generic distinctions and considers



that the most reasonable view to take is that we are dealing here with one species which is endowed with a remarkable capacity for variation.

Accepting this view, it may be said that *Filograna implexa* has been found in the Arctic Seas, off the British and Norwegian coasts, in the Mediterranean and Red Seas, in the Indian Ocean, and in Australian waters—a remarkably cosmopolitan distribution.

CHAPTER X

CORAL ALGAE

“Coralline is in a manner wholly spent among us to kill worms in children and in elder persons, and as the matter so the manner, but by what quality it worketh this effect is not declared by any, for it is altogether insipide and without taste of heate or cold as Corall itselfe is and if Corall be so much commended against the stone and fluxes, crampes, the falling sicknesse and melancholly etc. as you shall heare in its proper chapter doe not thinke but these may conduce somewhat thereunto also.”—JOHN PARKINSON, *Theatre of the Plants*, 1640, p. 1296.

A GREAT many kinds of marine Algae have their cell walls strengthened by deposits of calcium carbonate. Some of these retain the softness of texture and the flexibility of the non-calcareous Algae and could not possibly be mistaken for anything else than seaweeds ; but a considerable number assume such a hard texture and calcareous aspect that they are called corals not only by fishermen and sailors, but even, in familiar speech, by some men of science.

To separate these two groups of Algae is, of course, a thoroughly artificial proceeding and cannot be justified on any ground of vegetable morphology, but as the object of this chapter is only to provide such information as will enable the student to distinguish the vegetable from the animal corals and to recognise some of the most important forms, an artificial classification of this kind must be employed.

The discovery, by Peyssonnel and Ellis in the eighteenth century, that many of the corals are animals led unfortunately to a wider and erroneous generalisation that all corals are animals.

Linnaeus wrote a note to the genus *Corallina*: “*Corallina ad regnum animale pertinere ex substantia earum calcarea constat, cum omnem calcem animalium esse productum verissimum sit.*” Ellis¹ himself was of the same opinion but was rather more cautious in expressing it. “What and where the link is that unites the animal and vegetable kingdoms of Nature, no one has yet been able to trace out; but some of these corallines appear to come the nearest to it of anything that has occurred to me in all my researches; but then the calcareous covering, though ever so thin, shows us that they cannot be vegetables.” Pallas² dissented from this view, and in his introduction to the *Corallinae* said that the whole of this genus should be handed over to the botanists. Whereupon Ellis replied in a long letter to Linnaeus, which was published in the *Philosophical Transactions of the Royal Society* in 1767, that they were unquestionably animals.

Lamarck (1816) included all the calcareous Algae in his book on *Animaux sans vertèbres*, but his most noteworthy contribution to the subject was the introduction of the word “Nullipores,” which was accepted as a convenient term for corals that did not show conspicuous pores. The name was extended in its application in later years but finally abandoned altogether when it became too vague and indeterminate.

Some time before the year 1819 Targione Tozzetti recognised that the corals belonging to the genus *Halimeda* were plants, for he included them in his unpublished “*Catalogus vegetabilium marinarum.*” Phillipi (1837) and Unger (1858) proved that the greater numbers of the so-called Nullipores are *Lithothamnium* and therefore plants. And finally, in 1877, Munier-Chalmas recognised that the last remaining family, the *Dactyloporidae* (*Dasycladiaceae*), are calcareous Algae.

The study of calcareous Algae has revealed the fact that marine plants belonging to widely separated groups of Algae

¹ John Ellis, *Natural History of the Zoophytes*, 1786, p. 110.

² *Elenchus Zoophytorum*, p. 418: “*Mihi vero totum hocce genus Botanicis reliquendum videtur.*”

have the power of strengthening their walls with calcium carbonate, and thus assume an appearance superficially like that of the animal corals.

It is difficult to estimate the important part that is played by the calcareous Algae in building up and protecting the coral reefs of the tropical sea, but it is not perhaps so well known that they are found in such immense quantities at the bottom of the shallow seas in extra-tropical regions, including those of our own coasts, that they must influence, to some degree, as in other climes the complex forces that determine the fluctuations of the coast-line.

CLASS RHODOPHYCEAE

FAMILY CORALLINACEAE.—The most important of the algal corals are undoubtedly those belonging to this family of the red seaweeds. Some of them build up great encrusting masses on the surface of other coral or rocks, others are in the form of free knolls which are rolled over by the tide so that all sides may be exposed at different times to the necessary influence of the sunlight ; others again are attached to a foreign substance but give rise to dichotomously branching dendritic growths.

In some regions of the world these Algae occur in such enormous quantities that it is no exaggeration to say that they constitute the floor of the sea.

In the course of the voyage of the *Siboga*, for example, a bank of these corals off the Island of Haingsisi near Timor was exposed at low water and was described by Madame Weber van Bosse¹ as follows :

“ The Lithothamnion bank struck me because it is such a unique sight to see the ground, as far as the eye can reach, covered by the pretty beautifully pink-coloured knolls, which are heaped up so close together that, while walking, one crushes them continually, making a peculiar noise as of broken china.”

The first observation to be made in determining the systematic position of a coral that may belong to the

¹ *Corallinaceae of the Siboga Expedition*, livr. xviii. 1904, p. 5.

vegetable kingdom is the examination of the surface of a dried specimen with a magnifying glass. If the surface is found to be entirely imperforate and seems to be smooth and even greasy to the touch, it is certainly a plant and not an animal coral. It is probable, however, that no coral has a surface which is really imperforate, and if a little chip of the surface of such a coral be examined with a high power of the microscope, the minute apertures of the superficial layers of cells may be discovered. The coral Algae, however, may be in fructification, and in that case the surface will exhibit a number of more or less prominent convexities—projecting conceptacles—and at the summit of each of these convexities there is a pore of larger size, that is to say a pore visible under a low-power magnifying glass (Fig. 101). In such cases, if there is any doubt as to the nature of the coral, the hard close texture of vegetable coral—if it belongs to the Corallinaceae—and the characteristic cellular structure, when seen in section under the microscope, are sufficient to separate it definitely from any kind of animal coral and establish it as a plant. The next observation to make presents no difficulty and does not require the help of the magnifying glass. It is to determine whether the thallus is continuous in growth or jointed (compare Figs. 102 and 106). If it is continuous in growth it belongs to one section of the family Corallinaceae, which may be called section A. If it is jointed it belongs to the other section (B) of the Corallinaceae or to another Order of Marine Algae (see p. 210).

Section A of the Corallinaceae has been divided by systematists into a large number of genera and sub-genera, many of which are comparatively rare and will not be referred to in this chapter. The most abundant and widely distributed of the unjointed Corallinaceae belong to the genera *Melobesia*, *Lithothamnion*, and *Lithophyllum*.

The thalli of these three genera are so variable in form that it is difficult to give any general definition of any one of them that can be relied upon as a guide to the ready determination of any given specimen. Many overlapping forms occur which can only be definitely placed in their

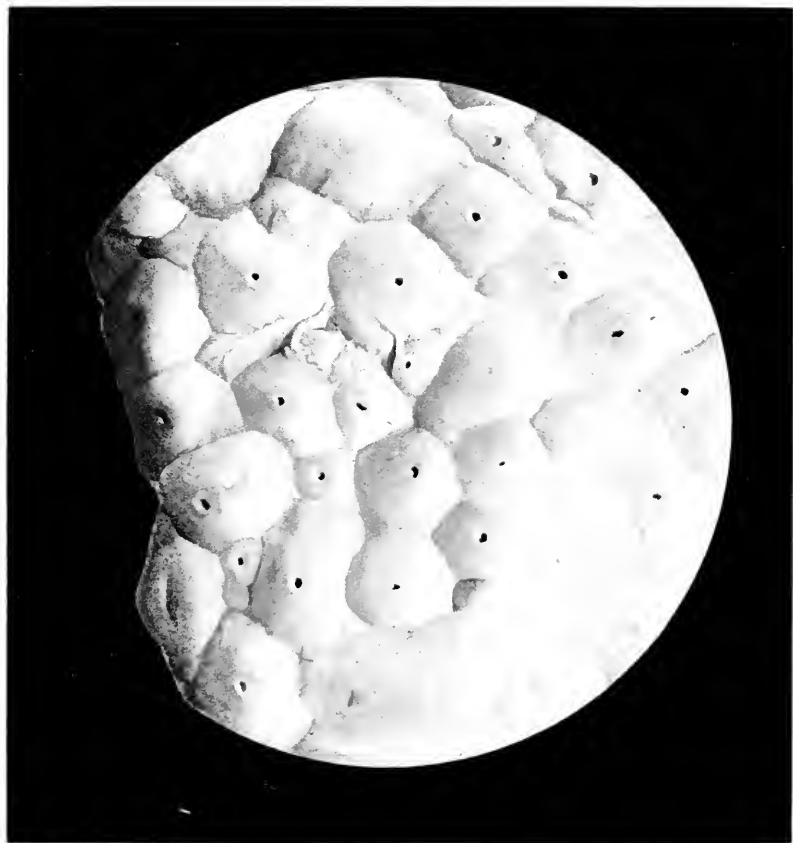


FIG. 101.—Surface view of a *Lithothamnion* showing the blister-like swellings and pores of the conceptacles. $\times 20$ diams.

systematic position by the skilled examination of the expert in the group.

MELOBESIA.—The genus *Melobesia* consists of a number of species which are usually found encrusting rocks or stones or epiphytic on other Algae. They consist of thin plates frequently round in outline, following closely the form of their support and often fusing laterally with neighbouring thalli to form continuous plates of considerable extent. At the surface there may be seen prominent rounded or conical protuberances which contain the conceptacles, and these are perforated when ripe by a single median aperture. The greater part of the thallus of *Melobesia* is only one layer of cells in thickness, and as the members of this genus do not increase in size vertically they never form thick massive structures. It is only in the regions of the conceptacles that the thallus is more than one layer in thickness.

There is one other character of importance that is of assistance in the recognition of *Melobesia*, and that is the presence of small hair-like processes which project from the surface of the ordinary (*i.e.* not conceptacular) parts of the thallus, giving the surface a somewhat velvety texture.

This last character separates the genus *Melobesia* from *Heteroderma*, which in other respects it closely resembles.

There are about sixty species of *Melobesia* and *Heteroderma* widely distributed and often very abundant in the tropical and temperate seas of the world.

LITHOTHAMNION.—The genus *Lithothamnion* is even more widely distributed and abundant, and the numerous species exhibit an immense variety of form and structure, some being encrusting plates, others forming papillate clumps or free knolls, and others again growing into small branching shrubs.

This genus can usually be distinguished from *Melobesia* by the thickness of the thallus, which always consists of several layers of cells, but confusion may arise between larger specimens of *Melobesia* and young *Lithothamnions* unless a critical examination of the microscopic structure is made. The distinction between *Lithothamnion* and *Lithophyllum*

is more difficult, but reference to that will be made at a later stage.

The most familiar form of *Lithothamnion* is perhaps the flat encrusting species (*L. lenormandi*) frequently found encrusting stones and rocks at low tide on the British coasts. It is usually of a dark salmon-red colour but becomes pink or blanched when exposed to the sunlight. In deeper water off our coasts another species (e.g. *L. fasciculatum*) may be found, sometimes in immense quantities, forming a complete carpet over considerable tracts of the sea-bottom.



FIG. 102.—*Lithothamnion dimorphum* from west coast of Ireland. Nat. size.

This is a branched fasciculate form.

Another form such as that represented by *Lithothamnion dimorphum*, also found off the British coasts, consists of large irregular lumps of coral several inches across with a surface covered with short papillate or mammillate processes (Fig. 102).

The importance of *Lithothamnion* lies in its widespread distribution and extraordinary abundance. Thus on the coast of Spitzbergen and Nova Zembla, *Lithothamnion glaciale* covers the bottom in deep layers for several miles. *L. ungeri* forms banks off Greenland. In temperate regions we have the *Lithothamnion* beds on the British coasts and such instances as the Nullipore banks of the Gulf of Naples, which are mainly composed of *Lithothamnion ramulosum*.

In the Tropics, reference has already been made to the abundance of *Lithothamnion* on the reefs of Timor. Off Tahiti rounded masses of this coral were found in 10 fathoms of water in such abundance that the dredge came up filled with them. Gardiner has also referred to its

occurrence in large quantities in various localities in the Indian Ocean.

Many other examples could be given to illustrate the wide distribution of this genus of calcareous Algae and of its importance in forming and protecting the bed of the sea in shallow waters. It extends from the Arctic seas to the coral reefs of the Tropics, and wherever the conditions of the tides and sea-currents are favourable for its growth, whether in the cold waters of the arctic regions or the warm waters of the equatorial regions, it seems to dominate the position.

LITHOPHYLLUM.—The genus *Lithophyllum* is another calcareous Alga which is usually found encrusting rocks, corals, and other animal and vegetable growths, following the irregularities of its support and throwing up papilliform or dome-shaped tubercles from its upper free surface. It frequently becomes free by detachment from its original support and then forms spherical or irregular lumps that are rolled by the surf. Like other Rhodophyceae the living coral has a pink or red colour, but specimens of *Lithophyllum* which are dried and dead are nearly always white in contrast to the specimens of *Lithothamnion*, which when dried usually but not always retain a reddish colour. The specimens of this genus often attain to very great dimensions, and on some of the coral reefs of the Tropics form huge, massive or encrusting growths covering the greater part of the rocks exposed to the breakers. There can be no doubt whatever as to the very important part that is played by Algae of this genus in the building up of the coral reefs, and in protecting them from wave action and other destructive agencies.

The genus *Lithophyllum* is more prevalent in the warmer than in the colder seas, but specimens are found in all the great sea areas, *e.g.* *Lithophyllum* (G.) *brassica florida*¹ in the Mediterranean and *Lithophyllum lichenoides* of the British seas.

It has already been mentioned that there is no character which can be readily determined by the field naturalist or

¹ I have included in this account of *Lithophyllum* the species attributed to the genus *Goniolithon* by Foslie. *Vide infra*, p. 205.

traveller and used by him to distinguish a *Lithophyllum* from a *Lithothamnion*. There is so much variation in size and form in both genera, and colour is such an untrustworthy guide to generic distinctions, that there are many specimens which can only be determined by experts in the group. Nevertheless, there can be no doubt that when critically examined the genera are distinct, and a few words may now be written to indicate the nature of the characters by which they are separated. When a thin section of a part of a thallus of one of these genera is examined, it will be found to consist of many layers of minute cells with thick calcareous walls (Fig. 103). The cells are roughly cubical

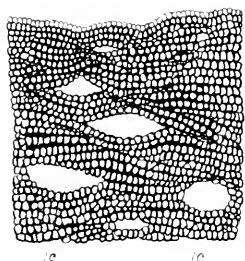


FIG. 103.—Section of a piece of the thallus of a *Lithophyllum* showing the cells (about 0.02 mm. in breadth) with thick calcareous walls and the surface (c, c) representing the gaps formed by old conceptacles. 50 diams.

in shape and somewhere about 0.02 mm. in breadth. The layers of cells are not uniformly arranged except in very young growths, but exhibit oval or spherical gaps that represent the spaces in which the conceptacles were placed. These gaps may be about 0.1 mm. in length.

There are three kinds of conceptacles, one kind containing the tetraspores or asexual reproductive bodies, a second kind for the antheridia or male reproductive organs, and a third for the female reproductive bodies (archegonia or cystocarps). It seems probable that no one specimen or frond of a specimen bears more than one of these kinds of conceptacles at the same time. The ripe sexual conceptacle in both genera is roughly dome-shaped in vertical section, the dome usually indicated at the surface by a convexity perforated in the centre by a pore, and it is extremely difficult to distinguish the sexual conceptacles of the one genus from those of the other by any characters that persist in the dried coral. The young tetrasporangial conceptacles, however, do show an important difference. In *Lithothamnion* they are perforated by several

pores at the surface (Fig. 104), in *Lithophyllum* by only one (Fig. 105).¹

Another difference between *Lithothamnion* and *Lithophyllum* has been described. In the former there is a marked distinction between the outer layers of small cubical cells constituting the Perithallium and the inner layers of larger and longer cells constituting the Hypothallium. In *Lithophyllum* the hypothallium is represented by a single layer of cells or is entirely wanting.

Enough has been said, perhaps, to indicate to the reader that there is a scientific distinction of some importance between these two genera, and that the accurate determina-

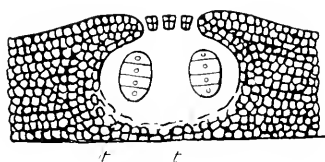


FIG. 104.—Section of a tetrasporangial conceptacle of a *Lithothamnion* showing two tetraspores (*t*, *t*), and the surface perforated by several pores.

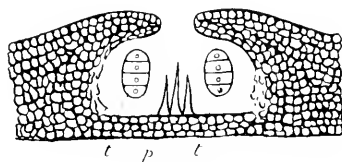


FIG. 105.—Section of a young tetrasporangial conceptacle of a *Lithophyllum* showing two tetraspores (*t*, *t*), the surface perforated by one pore and a tuft of paraphyses (*p*) at the base.

FIGS. 104 and 105 from Engler and Prantl.

tion of the character that separates them requires some special skill and scientific appliances.

It has been noted (p. 203) that many of the species of the old genus *Lithophyllum* have been separated by Foslíe into a new genus *Goniolithon*. The difference between these two genera lies in the character of the asexual conceptacle. In *Goniolithon* the tetrasporangia are evenly distributed over the floor of the conceptacles, whereas in *Lithophyllum* they are formed only on its sides, the centre of the conceptacles being provided with papilliform processes called the Paraphyses (Fig. 105).

¹ For further information on this point see A. Engler and K. Prantl, *Die natürlichen Pflanzenfamilien, Nachtrag*, 1911; Nicolls, *University of California Publications: Botany*, vol. iii., 1908; and Mme. Paul Lemoine, *C. R. Paris*, Feb. 15, 1909.

There are two more coral Algae belonging to the family Corallinaceae to which some reference must be made, although neither of them play the same important part in the construction of reefs and sea-bottoms as the corals that have just been described.

They belong to the Group B (see p. 200) of coral plants which show a discontinuous deposit of calcareous matter so that both stem and branches consist of a series of calcareous joints linked together by non-calcareous internodes. This is the same "admirable contrivance of Nature" that has previously been described in the Alcyonarian genus *Isis* to protect the plants from the violent motions of the sea (see p. 121).

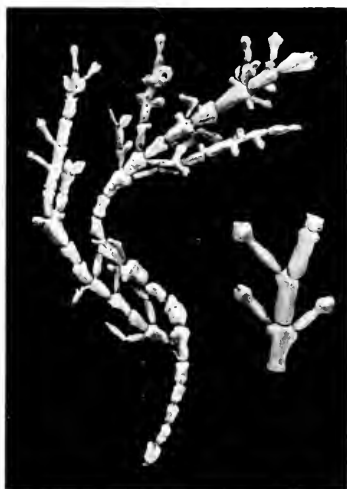


FIG. 106. — *Amphiroa californica*. Nat. size. The fragment on the left shows the swollen conceptacles at the ends of the branches.

AMPHIROA. — The first of these is *Amphiroa* (Fig. 106), a genus having a wide distribution in tidal and shallow waters of tropical and subtropical seas. In many localities, such as on the southern coast of California, a species of *Amphiroa* (*A. californica*) occurs in enormous quantities in sea pools at low water, and

masses of it are thrown up on the beach by the waves. The miniature forests of this bright purple-red coral which cover the rocks in the shallow pools and form a shelter for a great variety of little fish, crustacea, and other interesting kinds of animal life, are in the bright sunshine the scene of a wonderful display of brilliant colours equal only to what may be seen on a greater scale on the coral reefs.

Although *Amphiroa* exhibits considerable variation in size and in manner of growth, the plants are rarely more than five or six inches in height, the joints being 3-6 mm.

in length. They usually branch dichotomously in one plane, and the joints are flattened in the same plane and sometimes expanded. There are some species, however, in which the joints are cylindrical, as in *Corallina*.

The joint of an *Amphiroa* has the same hard texture and the same smooth and greasy surface as the *Lithothamnion* group of genera, and an examination with a lens does not reveal any pores or other apertures, except the openings of the conceptacles on those joints that happen to be ripe. It is therefore typically a Nullipore.

On microscopic examination of a joint, it is found to consist of an enormous number of minute cells similar to those of *Lithothamnion* although arranged rather differently. The nodes are composed of two or more rows of these minute cells covered by a cortical layer of similar cells differing from those of the joint in having very little or no calcareous matter deposited in their walls, thus allowing a certain amount of movement between one joint and the next.

The conceptacles are formed in small blister-like projections from the surface of the joints and are most conspicuous on the terminal branchlets of the plant.

CORALLINA.—Another member of the family *Corallinaceae* is *Corallina officinalis*, a common alga in the rock pools of our own coasts. Like *Amphiroa* on the Californian coast, it is frequently found to cover the rocks with a miniature forest of its slender delicate branches, of a pale pink or rose-pink colour. On account of this habit and of its diminutive size it was called by the older German writers the “Korallmoos” or “Coral moss,” a name which is very expressive of its habit and of the soft velvety texture it seems to have when felt by the hand immersed in the rock pool. But if this “moss” is dried and examined with a lens, the coral-white colour and the hardness of each separate joint reveal its true position as a member of the family to which *Amphiroa* and *Lithothamnion* belong.

It is a jointed coral like *Amphiroa*, and the joints are usually cylindrical in form, 1 mm. in length and 0.5 mm. in breadth.

The branching of the coral is in one plane and is usually trichotomous, two branches arising opposite one another from a joint of the main stem.

The conceptacles in this genus are in the form of prominent swellings at the terminal extremities of some of the branches, and the pore of each ripe conceptacle is at the apex of this swelling.

Some of the conceptacles, however, are found not at the extremity but at the sides of the joints.

The genus *Corallina* seems to be most abundant in the temperate regions, being very common on the coasts of Great Britain, France, and North America. It occurs in great quantities in some localities in the Mediterranean Sea, where *Amphiroa* is also found.

In former times this Coralline was collected, dried, and sold in the shops for medical purposes, but it was not considered to be so potent as the more expensive red coral.

The deposit of calcareous salts in the tissues of marine Algae is not confined to the genera of the family Corallinaceae, although it is in that family alone that we find the hard massive growths that form a conspicuous feature of the coral constituents of a coral reef.

It would take us far beyond the limits assigned to this chapter if any attempt were made to describe and classify all the calcareous Algae, but a short statement may be made concerning one of the calcareous Red Algae which is extremely abundant on some coral reefs and may serve as an example of quite a different type of structure.

FAMILY CHAETANGIACEAE.—The genus *GALAXAURA*¹ (Fig. 107) occurs in the Mediterranean and in the warmer seas of the Indian, Pacific, and Atlantic Oceans, and it forms dense clusters of profusely branching thalli attached to rocks and corals by tuft-like roots of branching filaments. The branches are usually cylindrical in form, and they are either not segmented at all or, if segmented, the segments or joints are not so pronounced or so regular as in *Amphiroa* or *Corallina*. The method of ramification, too, is quite different

¹ See F. R. Kjellman, *Kongl. Svenska Vet. Handl.* xxxiii. 1900.

from that of the other segmented coral Algae, being much more profuse, not confined to one plane, and very irregular.

It is in the structure of the plant, however, as seen with a lens, that *Galaxaura* differs from the other Algae that have been described most conspicuously. When it is fresh or preserved in spirit the branches show a smooth surface without pores or markings of any kind, but when felt with a needle or probe are found to be soft and yielding. When dried the calcareous framework seems to collapse, leaving

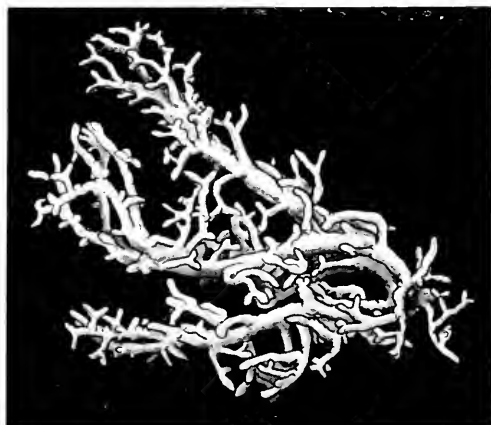


FIG. 107.—*Galaxaura*. Nat. size.

only flattened shrivelled strands of granular chalky substance cemented together by the dried vegetable tissues.

CLASS CHLOROPHYCEAE

This large and heterogeneous group of the green seaweeds includes a few genera in which the thallus is strengthened by the deposit of calcareous matter, and one of these—the genus *Halimeda*—is so widely distributed in the tropical seas and so abundant in many localities, that it must be regarded as an important constituent of the coral reef flora.

HALIMEDA.¹—This plant consists of a short stem which

¹ For a full account of this important genus see E. S. Barton, *Siboga-Expeditie*, livr. 2, 1901.

gives rise to a number of branches usually arranged in one plane, and is attached to the sand in which it grows by a mass of long branched filaments.

The stem and branches are composed of a series of calcareous internodes with uncalcified nodes, and are consequently very flexible (Fig. 108). The joints are frequently flattened and may be round, circular, kidney-shaped, triangular, or cylindrical in form. The individual plants vary a great deal in size, but the majority of the common varieties are not more than a few inches in height.

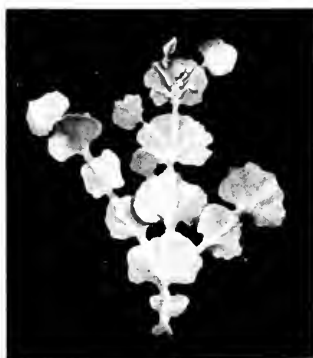


FIG. 108. — *Halimeda opuntia* from Hulule Male, Indian Ocean. Nat. size.

In life these Algae are grass-green in colour, but when dead become white and break up into coral-like beads or flakes.

In anatomical structure *Halimeda* is quite different from the Lithothamnion group of corals and their allies, and the principal differences can be easily recognised both in the dried calcareous skeletal structures and in the soft tissues, which can be seen, with the help of a simple magnifying glass, when the calcium carbonate is dissolved away with acid.

If a dried internode be examined it will be found to be rough to the touch, not smooth and greasy like a Lithothamnion, and it is so brittle that it can be crushed between the finger and thumb. With a lens the surface is seen to be perforated by a number of round pores about 0.014 mm. in diameter, regularly arranged at equal distances apart (Fig. 109). In this respect, therefore, although *Halimeda* is undoubtedly a plant, it is not a Nullipore. When seen in section these pores are found to be the mouths of short cylindrical

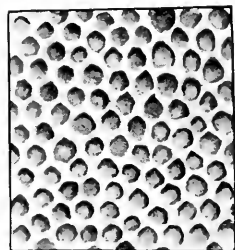


FIG. 109.—Surface view of *Halimeda opuntia* when dried. $\times 150$ diams.

cups perforated at the base by a minute aperture which brings them into communication with the labyrinth of spaces in the calcareous matrix of the internodes. The surface pores are therefore continuous with tubes of a lesser diameter which penetrate to the middle of the internodes. This is a feature of some importance, as it is unlike anything that is found in the calcareous structures of animal corals.

When a piece of fresh or preserved *Halimeda* is placed in a weak acid and the calcareous matter dissolved, the substance of the plant that remains is found to consist of a bundle of long tubes, sending off a number of branches to the periphery of the internodes and continued into successive joints through the soft uncalcified nodes. The fine branches of these tubes terminate in swollen cylindrical extremities which are arranged parallel with one another, vertical to the surface, and fit into cups of the calcareous skeleton previously described.

These terminal swellings of the branches are usually called the "peripheral cells" although the term "cells" is technically inaccurate, for *Halimeda* and its allies are not strictly cellular Algae, the filaments or tubes of which they are composed being continuous and not broken up by numerous cell walls into cell units. Whether we should call these Algae "non-cellular" or "unicellular," or adopt an altogether distinctive term, is a matter of controversy that can be safely left in the hands of the botanists.

The characters of *Halimeda* that have been described are sufficient to justify the separation of the genus from the *Lithothamnion* group.

It belongs to the group of the Chlorophyceae or Green Seaweeds and to the family Codiaceae.

The genus *Halimeda* is widely distributed in the tropical seas of the West Indies, Indian Ocean, and Pacific Ocean, but also occurs in the Mediterranean Sea and south of the Tropics, on the west coast of Australia, and the east coast of Africa.

The most widely distributed species is the *Halimeda tuna*, the original *Opuntia marina* or *Corallina opuntia* of the earlier writers. It is the common species of the

Mediterranean Sea, but is also found in shallow water in many parts of the Tropics. Being a green plant and therefore dependent upon direct sunlight, as are all the Algae, it cannot live in very deep water. Gardiner found it alive at a depth of 55 fathoms in the Indian Ocean—not far from the extreme limit of its bathymetrical distribution; but as it is comparatively light in texture and easily broken up by wave action, the dead fragments and isolated joints are frequently washed away into deep water and form there an important constituent of the sea-bottom. Thus Darwin¹ states that, off Keeling Island, at a greater depth than 90 fathoms the bottom was thickly strewn with joints of *Halimeda*.

But it is in the shallow waters of the lagoons, or among branches of coral on the reefs protected from the rough and tumble of the breakers, that *Halimeda* principally flourishes and adds its quota to the calcareous deposits of the tropical seas.

Two other genera of calcareous Algae belonging to the same family may be mentioned.

PENICILLUS is a beautiful little coralline Alga from one to four inches in height consisting of a cylindrical stem, attached below to the mud and sand in which it grows by a fibrous root mass, and terminating in a brush-like tuft of free filaments. The shape of this plant has led to the popular name for it of “the Merman’s shaving brush.” The genus seems to be widely distributed in the tropical seas, but very common in certain localities in the West Indies.

TYDEMANNIA has only recently been described from shallow water in the Malay Archipelago and Indian Ocean. It is a remarkably interesting little form consisting of a moniliform stem and branches, dividing up into a complex of twisted tufts or groups of fan-shaped branchlets terminating in long cylindrical filaments.²

¹ C. Darwin, *Coral Reefs*, p. 117.

² For further information on these genera and other calcareous Codiaceae see A. and E. Gepp, *Codiaceae of the Siboga Expedition*, livr. lvi., 1911.

CHAPTER XI

CORAL REEFS

"There is a great quantity of a kind of white coral on the shore, between Galle and Matura and many other coasts in the Indies. . . . There are large banks of this coral ; it is porous, neither so firm or smooth as the upright which grows in small branches ; and when they are come to the full growth, there grow others between them and then upon these grow others till it is become like a rock for thickness."—MR. STRACHAN, *Phil. Trans. Roy. Soc.* vol. xxiii., 1702, abridged edition, p. 711.

It is not surprising that the coral reefs of the tropical seas have arrested the attention and excited the interest of navigators and travellers of every generation. The white rollers breaking on the barrier of corals and the calm, pale blue water of the lagoon were emblems both of danger and of safety to the earlier navigators ; the abundance and variety of animal and vegetable life which the naturalist saw through the clear water as he passed over the shoals in his boat promised surpassing richness for his collections ; and the brilliancy of the colours of the coral polyps and of the varied fauna and flora associated with them was an ever-recurring delight to any one endowed with a sense of beauty in Nature.

But that is not all ; for, as the facts became known, many questions arose in the minds of the philosophers as to the origin of these reefs and the meaning of their many physical peculiarities ; and it soon became clear that the answers to these questions could only be given by the solution of problems of absorbing interest but of extreme perplexity and difficulty.

In the study of coral reefs we have a series of natural phenomena and a number of biological and geological problems which could only be dealt with adequately in a separate volume or series of volumes. But an outline sketch of them must be attempted here because they represent one of the principal objectives to which the study of the several classes of corals inevitably leads.

We may look upon the Madreporcs and the Milleepores, the Nullipores and the Astraeids, and even the Gorgonias and the Foraminifera, as the bricks and mortar with which the great mansions of the coral reefs are built ; and our task is not complete if, having studied the bricks and mortar, we do not consider the structure of the house as a whole. Moreover, the coral reefs, like mansions, are inhabited, and the study of the inhabitants—the fish, prawns, starfish, worms, and many others—and their relation to the structure which they frequent, cannot be entirely neglected even in an introductory chapter on the greater subject.

It may be remembered that, although the structures known as coral reefs are confined to the waters of the tropical belt, the corals have an almost world-wide distribution in the sea. Many examples of corals found within the British area have been described. Tangled masses of coral of great size are dredged up from some localities of the Mediterranean Sea. The cold waters of the Norwegian fjords yield a harvest of large massive corals of various kinds, and in the great depths of the ocean where the temperature is little above freezing-point, corals are often found.

But these corals occur usually as isolated individuals or in relatively small patches, and it is only under the tropical conditions of warmer water and more intense sunlight that “when they are come to their full growth there grow others between them and then upon these grow others till it is become like a rock for thickness.”

The coral reefs are as varied in their contours, in their composition, and in their distribution as the dry land itself, and the customary classification of them into fringing reefs, barrier reefs, and atolls is nothing but an artificial aid to

description and does not represent any sharp distinctions in Nature.

But when a reef is situated only a few score of yards from the shore, and separated from it at low tide by sand-banks and boat channels, it is called a "Fringing reef." When the reef is a mile or more from the coast-line and separated from it by a lagoon with a few fathoms of water at low tide, it is called a "Barrier reef." An atoll is a circular, oval, or more irregular shaped island or chain of islands in the open ocean composed of recent coralline limestone raised a few feet above the level of the sea at high tide and fringed on the outer side with coral reefs.

There are many intermediate forms between these three varieties. Thus a fringing reef at one part of a coast-line may be continuous with a barrier reef further along the coast, and it would be difficult to say at exactly what spot the one type merges into the other.

In the Pacific Ocean there are many examples of more or less conical islands surrounded by a barrier reef; there are cases of a very small central island surrounded by an atoll-like barrier reef, and then there are the more typical atolls without a central island. There is evidently in Nature a complete series of these forms, and there is no sharp distinction in type between a small island with a barrier reef and an atoll. There are also many different kinds of atolls. There is the typical ring-shaped island with a central shallow lagoon; there is the ring-shaped island with one or more breaks in it, through which the tides rush backwards and forwards from the lagoon to the open ocean. There are the half-ring or quarter-ring atolls with a group of reefs or islets representing the other parts of the atoll awash at high tide. And then there are the huge banks in the Indian Ocean, one hundred miles or more in length, as seen in the Maldivé and Laccadive Archipelagoes, which present the appearance of an atoll of atolls, an enormous ring of atolls enclosing an immense lagoon perched on the edge of a submarine bank that rises from the deep water of the ocean.

Each of these reefs consists of a great variety of living

and dead corals, and supports a rich fauna of fish, crustacea, starfishes, and holothuria, sea-worms, and smaller invertebrate organisms, as well as a flora of seaweeds; but no two reefs seem to be exactly alike, and the complex of natural forces that plays upon them leads to the abundance of some kinds of corals on this reef and to their suppression on that, to the richness and vigour of growing corals in countless masses, or to the accumulation of quantities of dead and decaying lumps of coral among a relatively few surviving living ones.

The first impression of one coral reef may be that it consists of nothing but huge shrubs of stag's-horn Madrepores, of another that it is all palmate Madrepores, of a third that it is all Lithothamnion, although a closer examination shows that many other kinds of coral occur among the prevalent forms. In other places, however—and this seems to be the case particularly on the fringing reefs—the corals of different species are more evenly distributed, Madrepores, Porites, Millepores, Seriatopores, and other kinds being all mixed up together in such a way that it is difficult to say that any one species is predominant.

With such variety in the composition of the living coral reefs, any detailed account that may be given must be regarded as the description of a particular part of a particular reef and must not be considered applicable to the reefs in any other district. It is perhaps one of the greatest charms of coral reef work that it presents so much variety. As the naturalist surveys the fringing reef of a coast, he finds with every mile that he traverses a different grouping of the species of corals; he discovers new varieties here and there, he sees different kinds of fish and holothurians, he may even find abundance of some species which formerly he thought to be rare.

And as with the details of composition, so with the general effects. On some reefs he may be charmed with the richness and variety of the colours, on others disappointed with the almost uniform display of dull brown or dirty pink tones.

Coral reefs also differ very much from one another in what may be called their vigour or vitality. In some

places the reefs are built up almost entirely by living corals, sponges, and other marine organisms; there is not a space large enough for a human foot that is not covered with something alive. In other places, perhaps only a few miles away, the living corals are separated by massive boulders and smaller rocks and stones of dead and decaying coral, and the reef is scored by numerous irregular channels in which but few living things are to be found.

It is often very difficult to account for these differences in the vigour of the reefs. The corals require for their healthy growth certain conditions of temperature, light, food supply, freedom from sediment, and so on, which are difficult to measure and estimate. If all these conditions are favourable a healthy vigorous reef is the result, but if any of them are unfavourable some of the species of corals die, and perhaps in dying create other unfavourable conditions, until the reef itself shows signs of decay.

It is important to bear in mind that the coral reefs, unlike the rocks of the coasts of temperate climes, are liable to comparatively rapid changes in form. They may for many years continue to grow seawards, and then, owing to a change in the set of the currents that sweep the coast, or to some other cause, they decay and retreat backwards towards the shore. It seems probable that a reef never remains perfectly stationary. It is always slowly advancing or retreating, and with every movement it must affect in some degree the set of the sea currents on the coast and thus influence favourably or unfavourably the growth of the corals further along the reef.

It is like a huge living pulsating organism slowly stretching out an arm here and withdrawing one there, in some places showing youth and vigour, in others disease and death, capable of withstanding the rough buffetings of storms and surf and yet extremely sensitive to some of the slighter changes of environmental conditions.

In the growth and decay of the reefs there are many agencies at work both for the protection of the corals when alive and for their rapid disintegration when dead.

When a coral reaches a certain size the living tissues are

apt to die at the base, leaving the bare skeletal structures exposed to the attacks of various boring and otherwise destructive organisms. For a time they may be protected from these attacks by the overgrowth of many different kinds of encrusting animal and vegetable colonies.

Among these the most important, perhaps, are the hard calcareous structures formed by the coral Algae, Lithothamnion and Lithophyllum, which form at first a thin film covering the exposed parts and following its contours like a crust, and then later growing beyond its support to form a thallus of its own. It is often discovered, when a large lump of coral is examined, that it consists of a thick crust of one of these coral Algae covering a core of some kind of Madreporae, as if the Madreporae had been overwhelmed and smothered by the Lithothamnion. But it is a question which has not been satisfactorily answered whether there is really any real smothering process in the production of these lumps. It seems to be most probable that the encrusting Alga has simply followed the death of the living tissues of its host from its base until when the last polyp has died it completely surrounds and decently entombs it by its further active growth.

The coral Algae not only protect the individual Madreporarian and other more delicate corals from the onset of decay, but undoubtedly play an important part in welding them together to resist the action of the surf; and on many reefs where the breakers fall with great force they form, as it were, an advanced post of coral reef to protect and shelter the ranks of the others in the outer waters of the lagoon.

The exposed base and stems of corals are also protected by the growth of the pink discs of the Foraminifera, Polytrema, and Homotrema, by Cellepora and other Polyzoa, by various kinds of encrusting Sponges, by Tunicata, and sometimes by masses of calcareous worm tubes.

On the other hand, the exposed base of the coral may be attacked by several species of bivalve molluscs which bore great cylindrical tubes through its substance, by cirripedes, worms, sponges, and even filamentous Algae, which dissolve the calcium carbonate and form lesser tubes and cavities for

their shelter and protection. If in this struggle for existence the organisms which attack the base of the coral get the upper hand over those that protect it, the time soon comes when a strong wave causes the perforated base to fracture, the colony topples over and is cast up into the sand of the lagoon, where it is smothered or gradually falls down the outer slope of the reef into deep water, to form with its companions in misfortune a talus on which the living coral reef extends.

The broken bits of dead coral that are cast into the lagoon may be further comminuted by the strong teeth of many species of the coral reef fishes, by passing through the alimentary canals of the holothurians and various kinds of Sipunculid and Polychaet worms, and by the rolling action of the surf, until, at last, they are driven on to the dry land and contribute to the formation of those glistening white beaches which are so characteristic of the tropical shores.

A recent discovery by Drew¹ has shown that there is yet another element entering into the complex problems of the disintegration of corals and the formation of calcareous sands and muds, and that is the precipitation of amorphous calcium carbonate by the action of the denitrifying bacteria of the sea. In the Bahamas and Florida Keys large quantities of a chalky mud seem to be formed by this action, and it can readily be understood that if such mud, together with the corals and shells which it has covered, were raised above the level of the sea, it might in time become consolidated to form a hard rock similar to chalk or limestone. Further investigation of this important action in the Pacific and Indian Oceans will doubtless lead to important results.

The constant formation of sand and mud by the disintegration of coral is an important factor in the determination of the constitution of the reef. If it is washed away as soon as it is formed the corals can thrive, but if, on the other hand, it is deposited in the form of silt on any part of the living reefs, the corals may be killed.

¹ G. H. Drew, "On the Precipitation of Calcium Carbonate in the Sea by Marine Bacteria," *Papers from the Tortugas Laboratory of the Carnegie Institution of Washington*, vol. v., 1914.

There seems to be nothing more fatal to the growth of corals than this deposit of silt. The delicate polyps have some power of removing a few light foreign particles that fall upon them, but a continuous shower of grains of sand or mud hinders their powers of expansion, interferes with their capacity to capture and ingest their food, and by shutting off the light from the canal systems checks the photosynthetic action of the zoochlorellae. Any change in the set of the tides and currents that drives the silt on to a vigorous part of a reef, or causes stagnation and a fresh deposit of silt elsewhere, may be regarded as among the most destructive of the agents which check the growth of the reefs.

The study of the existing conditions on the reefs leads, then, to the conclusion that, in addition to the great constructive factors of coral growth, there are also destructive agencies at work which may check and destroy what has been built up when environmental circumstances change. There are probably no examples of homogeneous reefs that have shown continuous progress for long periods of time. The growth of a reef is a process of stages of active increase, of comparative stability, and in some cases of considerable reduction, the sequence and duration of these stages varying enormously in different parts of the tropical world.

It has been shown that in the building of the tropical reefs a great many varieties of corals take part. It is not the work of one genus or of one order of corals. There are perforate and imperforate *Zoantharia*, *Millepores*, *Alcyonaria*, and coral *Algae* in varying proportions contributing their quota to the formation of the great masses of coral rock. A critical examination of these corals proves that they are not the same as those found in more isolated patches in deep water or in the Mediterranean Sea, the Norwegian fjords, or other extra-tropical regions of the world.

It becomes a matter of some importance, therefore, in the consideration of the problems of coral reef formation, to collect the evidence that is available concerning the distribution in depth of those that can be roughly classified as reef-building corals as distinct from those that do not enter into the composition of the reefs.

Darwin estimated that the greatest depth at which the reef-building corals can flourish is between 20 and 30 fathoms, and he inferred from that estimate that the reefs could not have been formed by up-growth from a stationary sea-bottom of any considerable depth.

It is interesting to find that, as a result of the extensive investigations of more recent times, Darwin's estimate is confirmed and the conclusion is reached that reef-forming corals do not flourish at greater depths than 25 fathoms.¹ It is true that some genera such as *Madrepora*, *Porites*, *Millepora*, *Heliopora*, have been found alive at depths of 35-50 fathoms of water, but the conditions at these greater depths do not appear to be favourable to the formation of luxurious plantations. Some forms such as *Heliopora*, *Millepora*, and *Goniopora* are more frequently found in depths of over 20 fathoms than others, such as the *Seriatorporidae*, which are usually confined to quite shallow water, but there seems to be no doubt that they all flourish most abundantly in water of less than 25 fathoms.

The genus *Dendrophyllia* is one of the few reef-building corals which appears to be rarely found in water of less than 20 fathoms and to flourish in depths of 20-50 fathoms, and it is interesting that this genus is also one of the few corals that occur not only in the tropical seas but extend into the cooler waters of the Mediterranean Sea and Atlantic Ocean.

The coral *Algae*, *Lithothamnion* and *Lithophyllum*, which play such an important part in the constitution of some reefs, are sometimes left exposed at low tide even in the Tropics, but are more usually found in shallow water down to a depth of 40 fathoms²; but unlike the typical reef-forming corals, these plants have a world-wide distribution, occurring, sometimes in great abundance, not only in tropical seas but also in temperate and arctic waters.

The corals of the order *Styasterina* have a much greater range of distribution in depth than any of the true reef-

¹ J. Stanley Gardiner, *Fauna and Geography of the Maldive and Laccadive Archipelagoes*, vol. i. pt. 3.

² Madame Weber van Bosse in *Science of the Sea*, edited by G. H. Fowler, 1912, p. 152.

forming corals. The genera *Distichopora* and *Stylaster*, for example, are not uncommonly found in quite shallow pools at low tide in the Tropics, but species of *Distichopora* are found at a depth of 100-260 fathoms in the Indian Ocean and the West Indies, and species of *Stylaster* are found in the Malay Archipelago in depths of 0-1038 fathoms.¹ The other genera of this Order are principally confined to deep water.

The reason for the limited distribution of the more important reef-forming corals cannot be determined with certainty. It may be that their lateral distribution north and south of the tropical zone is checked by the lower temperature of the water, a minimum temperature of about 18° C. being necessary for their continued existence.

The range in depth may be determined by the power of direct sunlight to penetrate sea-water. There can be no doubt that the coral Algae are entirely dependent upon sunlight for their continued vitality, and if a depth of 40 fathoms be taken as the maximum depth at which living coral Algae are found, it will be found to agree with the maximum depth at which effective rays of the sun can penetrate sea-water. The other reef-forming corals are not, perhaps, so entirely dependent on sunlight as the coral Algae are, for they are provided with tentacles and other organs for catching and digesting animal food ; but still, a majority of them are also provided with the chlorophyll-bearing zooxanthellae which require sunlight, and it is highly probable that these corals do not flourish unless their animal food is supplemented by the food supplied by the zooxanthellae. In support of this conclusion it may be pointed out that the *Stylasterina* which are not provided with zooxanthellae are independent of the action of direct sunlight, and extend from shallow water to the great depths of the ocean.

The rate at which corals grow has also an important bearing on many of the problems connected with coral reefs. On this point a great deal of interesting information has been collected in recent years. By the measurement of corals found on anchors and cables which were sunk at a known

¹ *Stylasterina of the Siboga Expedition*, livr. xix., 1905.

date, or of corals found in channels that had been cleared a definite number of years before, and by the measurement of actual specimens on the reefs after an interval of years, we are now in possession of some information which enables us to judge of the rate of the growth of corals in shallow water. Thus the branches of a Madrepore may grow at the rate of 1-2 inches in length in a year, and a great mass of Porites was found to have increased 30 inches in diameter in 23 years at the rate of nearly 2 inches per annum. There is probably very little uniformity in growth, the rate varying a great deal according to temperature, food supply, and many other natural conditions; but it has been estimated that under ordinary circumstances a reef might grow upwards from a shallow sea-bottom at a rate of one foot in $11\frac{1}{2}$ years, or $14\frac{1}{2}$ fathoms in 1000 years.¹

From the study of these general aspects of the recent coral reefs we may now pass on to the consideration of the greater geological problems of the origin of the atolls and of the various theories that have been advanced in the endeavour to solve them. The first serious attempt in this direction was made when Darwin² published his famous book on coral reefs, giving the results of his researches and reflections on the subject during the voyage round the world of H.M.S. *Beagle*. According to his theory all atolls and barrier reefs of the world originated as fringing reefs in shallow water off the coasts of tropical continental lands and islands. When the land subsided by earth movements and the shores became submerged the coral reefs, rising vertically as their supporting rocks sank, became separated from the retreating shore by ever-increasing distances. In this way the fringing reefs became converted into barrier reefs and the shallow sand-patched lagoons of the fringing reefs became deep-water areas. In the case of islands, if the land continued to subside until the island became entirely submerged, all that would

¹ For further information on these points see: J. Stanley Gardiner, *Fauna and Geog. Maldive and Laccadive Archipelagoes*, vol. i. Appendix A; and A. G. Mayer, "Ecology of Murray Island," *Carnegie Institute of Washington Publications*, vol. ix., 1918.

² C. Darwin, *Coral Reefs*, 1st ed., 1842; 3rd ed. edited by Prof. Bonney, 1889.

be left at the surface would be a ring of coral reef enclosing a deep-water lagoon.

The Darwinian theory is usually called the subsidence theory, because it postulates a gradual sinking of the crust of the earth over wide areas of the great ocean basins.

Since the time when Darwin wrote, a great many more facts have been ascertained concerning the character of the floor of the great oceans, on the structure and distribution of the upraised coral reefs of the tropical islands, and on the construction and topography of living coral reefs and atolls ; and many subsequent writers have expressed grave doubts that the subsidence theory is not sufficient to account for the occurrence of all barrier reefs and all atolls. Some indeed, such as Alexander Agassiz, who spent many years of his life in exploring and critically investigating the coral reefs in all parts of the world, have come to the conclusion that in no single instance can the presence of an atoll be satisfactorily explained by the subsidence theory.¹

It is possible that the truth lies between the two extreme views, and that some barrier reefs and atolls have been formed during subsidence and that others have been formed during long periods of quiescence or even independently of earth movements. Let us, then, consider very briefly some reasons which have been brought forward as arguments against complete acceptance of Darwin's hypothesis.

The discovery of great masses of coral reef situated several hundred feet above the sea-level, composed of the same genera of coral as now occur on modern reefs, on islands in the Pacific Ocean situated in close proximity to true barrier reefs, proves that this land has been actually elevated in geologically recent times, and it is difficult to reconcile this fact of elevation with a theory which demands long-continued subsidence in the formation of the neighbouring barrier reefs. Many of the typical atolls of the Indian Ocean are raised to a height of nine or ten feet above high-water

¹ Prof. W. M. Davis of Harvard University has recently given reasons for believing that the subsidence theory is sufficient to account for the occurrence of all atolls and barrier reefs (*The Scientific Monthly*, vol. ii. No. 4, 1916, and other publications).

mark. This was well known to Darwin, who accounted for it by the supposition that the dry land of the atolls had been formed by boulders of coral cast up by the waves in great storms. But if it had been formed in this way, the corals of which it is composed would be found lying in various positions, some upright, some on their sides, and some upside down. A critical examination, however, of some of these rocks has shown that the corals are all upright and in the position in which they grew on the living reef. This proves that even in the Indian Ocean, which was considered to provide the most conclusive evidence in favour of the subsidence theory, a recent elevation of a few feet has actually taken place.

The question of the foundation on which the atolls and barrier reefs rest is obviously an important one, and various attempts have been made to answer it by making deep bore holes through the coral rock.

Darwin considered that the many widely scattered atolls must rest on rocky bases,¹ and if it could be proved by boring that the atolls and barrier reefs do rest on rocky bases we should be in possession of the most conclusive evidence of the truth of the subsidence theory. But it has been shown that in very many cases the reefs rest not on a terrigenous base but upon a submerged platform composed of a hard limestone formed by calcareous organisms other than reef-building corals, which has been planed down by wave action in prehistoric times to a moderately level surface.

Sluiter² showed many years ago how it is possible for a coral reef to be formed even on the soft volcanic mud of the submerged slopes of Krakatoa, and borings through the coral islands Edam and Onrust led to the discovery that they rest on the muddy bottom of the Java Sea.

There seems to be, in fact, no direct evidence either from borings or soundings, or by the study of elevated reefs, of the existence of great thicknesses of coral rock, formed by the typical reef-building corals resting on a land foundation such as the Darwin theory of subsidence demands.

¹ Darwin, C., *Coral Reefs*, 3rd ed., p. 125.

² Sluiter, *Biol. Centralblatt*, ix. 1890, p. 738.

There is still another difficulty in the way of accepting the original form of the subsidence theory. The lagoons of the atolls and barrier reefs are not deep pits or troughs, but usually extraordinarily flat basins at a more or less uniform depth of twenty fathoms. If these reefs had been formed over long periods of time by gradual subsidence of a few thousands of feet, the lagoons would have been of greater depth and provided with sloping sides.

To meet some of these difficulties Sir John Murray¹ put forward an alternative theory which did not involve the hypothesis of a long-continued subsidence of the land. The discoveries made during the voyage of H.M.S. *Challenger* concerning the constitution of the floor of the great oceans and the nature of deposits on the sea-bottom, led him to the conclusion that a continuous rain of calcareous organisms from the surface-waters causes the formation of submarine banks, which from time to time rise to the level at which reef-building corals can thrive. When the plantations thus started reach the surface of the sea by upward growth they gradually assume an atoll form by the death of the corals in the centre and the outward growth, like a fairy ring, of the corals on the edge, the lagoon being formed subsequently by solution of the dead coral by the sea-water which percolates through the mass.

The barrier reefs are formed according to this theory by the outward growth of fringing reefs on a basis formed mainly by the talus of dead corals which are broken off the growing edge by storms, and the lagoon channels are formed in the same way, by solution, as the lagoon of the atolls.

This theory, of which only the briefest outline can be given here, has been very unfairly termed the "still stand" theory. It is true that it would account for the formation of the characteristic coral reefs on a perfectly stationary foundation; but Sir John Murray was fully aware of the probability of earth-movements both of elevation and subsidence, and his theory would hold good notwithstanding slow movements of this kind in either direction.

¹ Sir John Murray, *Proc. Roy. Soc. Edin.*, vol. x., 1879-80.

Murray's explanation of the formation of the deep lagoons by solution seems to be the least acceptable part of his theory, as it has been shown that in the coral seas the water does not contain free carbonic acid and there is definite evidence that in many instances the lagoons are slowly silting up instead of deepening, as they should do if they are subject to solution. Notwithstanding these objections, however, it is still possible that some of the lagoons have been formed, not perhaps by solution but by the scouring action of the tides, which do carry great quantities of the fine detritus formed by the natural disintegration of the corals through the channels into the deep water beyond the outer edge of the reefs.

There are two processes going on continuously in the lagoons, the accumulation of silt and the scouring action of the tides, and these, in general, counteract one another ; but it is probable that under changing conditions accumulations may at one time gain the upper hand and at another the scouring action may become dominant. The evidence that a particular lagoon is at the present day silting up, is, at any rate, no decisive proof that the lagoon has not formerly undergone a process of deepening by the scouring action of the tides.

The existence in many parts of the world of extensive submarine banks or platforms on which the modern coral reefs rest has been the basis of another theory of coral reef formation which has met with some support.

In the consideration of previous theories the question of any possible changes in the sea-level does not necessarily arise ; but it is clear that if the crust of the earth remained stationary and the level of the seas rose, the coral reefs and atolls might have been formed in precisely the same way as if the crust of the earth subsided and the sea-level remained constant.

It has been suggested¹ that during the Glacial Period so much water was piled up on the continental lands in the form of ice, that the level of the sea was lowered to the

¹ See R. A. Daly, "The Glacial Control Theory," *Proc. American Acad. Arts and Sci.*, vol. 51, 1915.

extent of about 30 fathoms. By this means large areas of sea-bottom were exposed which hardened to form limestones of varying constitution. As the ice melted and the sea-level rose these areas were again submerged and planed down to form the submarine platforms upon which, subsequently, the new coral reefs were formed.

If it could be definitely proved that during the Glacial Period in the northern hemisphere there was so much more water stored up in the form of glacial ice than there is at the present day as to cause a fall in the sea-level of 30 fathoms, there would be some foundation for this theory. But the evidence on that point appears to be far from conclusive. Moreover, the theory also demands that the submarine platforms on which the coral reefs rest should all be of the same (pleistocene) geological age, and evidence bearing on this point can only be obtained by the study of the foundations of reefs that have grown and subsequently been raised above the sea-level since that period. It may be some years before a sufficient survey of these upraised reefs in many parts of the world has been made to judge fairly of the evidence they afford on the glacial control theory, but Wayland Vaughan has shown that the great Florida plateau has existed since late Eocene times and that some of the West Indian platforms are at least as old.¹

The glacial control theory is extremely interesting and ingenious, but it does not appear to be likely to supersede entirely the other theories that have been briefly described. It may be proved that "glacial control" had some effect in producing the general structure and distribution of many of the modern and recently upraised reefs, but there can be little doubt that some of our modern reefs do not rest on a submarine platform formed in post-glacial times and that others rest on platforms that were certainly pre-glacial.

The conclusion that must be reached after a careful study of the literature bearing upon the subject is, that there is no general agreement among men of science upon any one theory of the origin of coral reefs. The controversy

¹ T. Wayland Vaughan, *Smithsonian Institution, Bull.* 103, 1919. This paper contains an admirable summary of coral reef theories.

continues, and as with increasing knowledge the problems concerned appear to become more and more complicated, demanding more extended investigations of ever-increasing difficulty and expense, it is impossible that a complete set of explanations of the phenomena will be discovered in our generation.

It has been suggested by some of the bitter critics of evolution that Darwin has been discredited by his theory of coral reefs. Nothing could be more absurd. The simple and beautiful theory which he expressed was the starting-point of a great scientific movement and has led to the discovery of an immense store of facts about the physical geography of the tropical seas of the greatest interest and importance. If it is borne in mind that at the time he wrote his famous book on coral reefs and islands our knowledge was far less than it is now, his work stands out as a model of scientific reasoning and inference.

The evidence afforded by the embayments of islands that are surrounded by barrier reefs, by the unconformable relation of elevated reefs to the rocks on which they rest, and by other geological considerations, appears to support the view that subsidence of the earth's crust in the coral reef zone has occurred over even a wider area than Darwin himself believed.

The doubts that have been expressed, as the result of more recent investigations, that solution or scouring could have produced lagoon depths of over 20 fathoms, appear to have turned the scale of opinion in favour of Darwin's explanation of these depths by subsidence.

The principal conclusion made by Darwin, which has not been confirmed, and will probably be abandoned, is that the reefs were formed by long-continued depression of the lands on which they rest, and are consequently, in some cases, a few thousands of feet in thickness. There is no evidence either from borings in modern reefs or from the study of elevated reefs of the existence of such vast masses of continuously formed coral rock. It appears much more probable that in most parts of the coral zone periods of subsidence of relatively short duration have alternated with

periods of elevation, and that coral reef formation has been stimulated, checked, or even stopped, in successive periods of time.

If it is necessary, then, to abandon a part of the theory of coral reefs suggested by Darwin, or to agree that his theory does not account for the formation of some reefs which have been investigated since his time, there is no reason whatever for rejecting the many interesting and important results of his investigations, or for under-estimating the marvellous skill with which he marshalled his facts and formulated his scientific conclusions.

CHAPTER XII

THE EARLY TRADE IN BLACK AND RED CORAL

"At this point I must pause in order to indulge in my instinct for rambling."—DE QUINCEY.

RED CORAL

FROM time immemorial red coral has been regarded as an article of commercial value not only on account of its colour, lustre, and texture, but also on account of its supposed mystical powers as a charm and as a medicament.

There can be no doubt that before the Christian era it was used by the Greeks, the Persians, the Indians, the Chinese, and by the Celtic races of Gaul, of Britain, and of Ireland ; and it is also quite certain that all the red coral that was used by these people in ancient times came to them by trade from the Mediterranean Sea.

The red coral of commerce (*Corallium nobile*) has a very limited distribution. It is not found on any of the coral reefs of the world, and in dealing with the early history of the trade in coral it is important to note that it has not yet been discovered in the Red Sea, the Persian Gulf, or the Indian Ocean. The principal fisheries of the red coral were those of the southern coasts of France, of the coasts of Corsica, Sardinia, and Sicily, and of the northern coasts of Africa from Tunis to the Straits of Gibraltar. In quite recent times there has been a small fishery of red coral off the Cape Verde Islands in the North Atlantic Ocean, but it may be said that the genuine red coral is confined to the Mediterranean Sea and a few localities west of it in the Atlantic.

Another kind of coral belonging to the same genus but to

different species has been found in abundance in certain waters off the coast of Japan, and, although this coral is sometimes red and is always of the same hard texture as the Mediterranean red coral, so that it can be and is used for ornamental purposes, the evidence seems to be quite conclusive that it was not exported from Japan until quite recent times.

There can be little doubt, therefore, that the early trade in red coral began in the Mediterranean Sea, and in all probability in the western part of it, and that it spread from there to the distant parts of the world, where it was prized by the natives.

From the earliest times of which we have any record, red coral was supposed to possess certain magical properties, and was used not only for ornamental and decorative purposes but to ward off evils of various kinds, to still tempests, and to cure diseases.

The mythical origin of red coral is related in a poem by Orpheus of Thrace and by Ovid,¹ and may be briefly stated as follows.

When Perseus cut off the head of the Medusa and cast it on the sea-shore, the water-nymphs threw small branches of seaweed at it just for the fun of seeing them turn into stone. The seeds of these twigs when returned to the water gave rise to the coral, which even to this day turns into stone when it comes in contact with the air, although it is soft so long as it is still submerged.

Minerva was so pleased with the exploit of her brother that she conferred upon coral a number of the most extraordinary virtues.

She next endowed the plant with virtue strange
And to its kind a lasting influence lent
To guard mankind on toilsome journeys bent,

¹ Ovid, *Metam.* iv. 747-753 :

At pelagi nymphae factum mirabile temptant
Pluribus in virgis, et idem contingere gaudent,
Seminaque ex illis iterant iactata per undas.
Nunc quoque curaliis eadem natura remansit,
Duritiam tacto capiant ut ab aere, quodque
Vimen in aequore erat, fiat super aequora saxum.

Whether by land their weary way they keep,
Or brave in ships the terrors of the deep.¹

It was given also the properties of an antidote to all manner of stings, poisons, and enchantments, of a protector of the crops from plagues of caterpillars, flies, and pests of various kinds, and of a universal drug to cure the diseases of mankind.

The belief in the properties thus conferred upon coral by Minerva spread with the trade to the most distant parts of the Old World, and persists among the peasants of many countries, in one form or another, even to the present day.

We have very little information concerning the use of coral by the Greeks, beyond the reference to it in the poem by Orpheus. In recent excavations on the sites of ancient Greek cities, no specimens of coral in ornaments have been brought to light. In the Royal Albert Museum there is a copy of a pair of earrings in each of which there is a large bead of pink coral. These earrings were found in the Crimea and are believed to be of Greek workmanship of the fourth century B.C.

Minns² states that corals have been found in the tombs of the ancient Scythians, and that it was the custom among the Asiatic nomads to adorn the flanks of creatures in their art work with blue stone or coral inlaid.

There can be little doubt, however, that both Greeks and Romans used coral in ancient times in the form of amulets of various kinds to ward off evils from children and to protect adults from real or imaginary dangers. Pliny says: "Haruspices religiosum coralli gestamen amoliendis periculis arbitrantur; et surculi infantiae alligati tutelam habere creduntur."

But neither the Greeks nor the Romans seem to have valued coral as an article of jewellery or for inlaid decorative work on swords, shields, breast-plates, or other objects in the same way or to the same extent as the Oriental races and the Celts, and thus it came about that a trade was estab-

¹ From a translation of the poem by Orpheus of Thrace by C. W. King in *The Natural History of Precious Stones and Gems*, 1865.

² E. H. Minns, *Scythians and Greeks*, 1913, pp. 65 and 268.

lished with these distant countries which consisted in an exchange of red coral for emeralds, rubies, pearls, and other articles more highly valued by the Mediterranean races.¹

The use of coral by the Jews in pre-Christian times may be inferred from two references to it in the Bible.

The texts in the English Version are :

"No mention shall be made of *coral*, or of pearls : for the price of wisdom is above rubies."—Job xxviii. 18.

"Syria was thy merchant by reason of the multitude of the wares of thy making : they occupied in thy fairs with emeralds, purple, and brodered work, and fine linen, and *coral*, and agate."—Ezekiel xxvii. 16.

There has been some controversy among scholars about the correct translation of the Hebrew word "Ramoth," which in the English Version is translated "coral." Most of the authorities seem to agree that the word "Ramoth" does mean coral of some kind ; there are differences of opinion as to whether it means "red coral" or "black coral."

Gesenius expressed the opinion that it means "black coral," because the word "Peninim," which in the English Version is translated "rubies," is apparently red coral, and considered that this view is confirmed by Lamentations iv. 7, in which the Nazarites are described as "more ruddy in body than rubies" (Peninim, *i.e.* than red coral). This view also seems to receive support from another consideration of the texts.

In the verse from Ezekiel, coral (*i.e.* Hebrew *Ramoth*) is associated with emeralds, purple, and brodered work, fine linen, and agate, articles of trade that must have come from the Far East, and according to some authorities the word "Aram" is wrongly translated "Syria," but should be "Edom," a port for transport from S. Arabia and India. Now, red coral could not have been imported from India or from any country south of Palestine, as it occurs only in the Mediterranean Sea, but black coral might have been

¹ "In the same degree that people in our part of the world set a value upon the pearls of India, do the people of India prize red coral" (Pliny, xxxii. chap. 11).

imported from any of the warmer waters of the Red Sea, Persian Gulf, or Indian Ocean (see p. 132).

In the verse from Job as it is translated in the English Version, it is difficult to see any reason why "rubies" should be specially selected for comparison with "wisdom." But bearing in mind the multiple and marvellous magical properties of red coral in addition to its beauty as a jewel, the translation of the verse according to the views of Gesenius may reveal a new meaning. It would read thus :

No mention shall be made of black coral or of pearls, for the price of wisdom is above red coral.

The black coral and the pearls imported from the South are here grouped together, and the more precious red coral from the West stands by itself as a symbol of the most valuable of worldly possessions.

Apart from these references to coral in the Bible, we have practically no information as to the use of coral by the ancient Jews.

There is abundant evidence of trade in coral with the Far East in times long before the dawn of the Christian era.

It seems probable that Persia was an important market for coral, for Solinus, in his reference to the coral from the Gulf of Genoa, says: "This substance according to Zoroaster has a certain potency and in consequence anything that comes from it is reckoned among health-giving things."

But the Persians not only used coral themselves but passed it on to the races further East as an article of trade, for in early Chinese annals it is stated that "coral is produced in Persia, being considered by the people there as their most precious jewel."¹

At the time of the Han dynasty, a century or more before the Christian era,² the Chinese were already well acquainted with coral as an ornament, and it was valued so highly that

¹ B. Laufer, "Sino-Iranica," Field Museum of Nat. History, Chicago. Publications No. 201, 1919, p. 523.

² According to Prof. Pelliot the earliest use of the word Shanhu (*i.e.* coral) is in a poem written by a Chinese scholar, Sseuma Siang-jou, who must have died about 117 B.C. (*Archives concernant l'Asie orientale*, 1920, p. 145, footnote).

an expedition was sent to the Mediterranean Sea to investigate and report upon the coral fishery.

In the course of the trade routes, whatever they may have been in those early times, from the Mediterranean Sea to China large quantities of coral were bought by various Asiatic races of the countries through which it passed.

In the cave of the thousand Buddhas, south of the Gobi deserts, Sir Aurel Stein found a number of paintings on silk in which red coral is clearly shown.

The references to coral among the treasures of Thibet and India are of a much later date, but it is very probable that it was valued by the inhabitants of those countries quite as early in history as it was by the Chinese.

Marco Polo, who made his famous and adventurous journey across the Asiatic continent in the thirteenth century, said that the coral that comes from our part of the world has a better sale in Keshimeer than in any other country. He also tells us that red coral was held in high esteem in Thibet, for the people delight to hang it round the necks of their women and of their idols.¹

Even to this day coral necklaces are among the most cherished possessions of the wealthy Thibetans and are included among the sacred treasures of the monasteries of that country.

In India generally it may be said that coral was widely used for ornamental purposes, being found in ancient rings, necklaces, and among the precious stones that adorned the thrones. Tavernier (seventeenth century) says that the common people wear it and use it as an ornament for the neck and arms throughout Asia and principally towards the North in the territories of the Great Mogul, and beyond them in the mountains of the kingdoms of Assam and Bhutan.

It is possible that the belief in some of its magical properties may have gone with the red coral into the regions of the Far East, as we find it recorded in the T'ang Annals as an article in the Chinese *Materia Medica* of that period, and in the time of the Manchu dynasty red coral was used as a

¹ H. Yule, *Cathay and the Way thither*, Hakluyt Soc., vol. i., 1866, p. 159.

sacrifice on the altar of the Sun.¹ On this point, however, our knowledge is very scanty. All that we do know for certain is that it was highly prized as an ornament by these people.

In Japan, red coral has been used for inlaid artistic work on medicine cases (Inro), netsukes, tassels, and sword hilts for several centuries. It is generally believed that most of this coral was imported, and the fact that the Japanese word for coral, "Sango," so closely resembles the Chinese word "Sanhu" or "Sangu" suggests that it may have passed through the Chinese markets.

However, at an early period, coral of a different species but of a similar quality as regards texture and colour was discovered in the bay of Tosa; but, according to Kitahara,² the fishery was carried on in secret and consequently very much restricted in output, because the Daimyo of Tosa was afraid that the coral might be commandeered by the Shoguns. In this connexion it is interesting to note that on some of the ornamental designs of the seventeenth century a branch of red coral is depicted in the hands or the net of a dwarf, curly-haired, dark, and prognathic fisherman, obviously not a native of Japan. This may have been designed to throw the Shoguns off the scent of a native fishery, but there is just a possibility that it has reference to another coral fishery in some distant country of which all other evidence has been lost.

It was not until the Meiji reform of 1868 that the prohibition on the coral fishery was removed and an extensive and lucrative export trade from Japan was developed.

The earliest reference that can be found on the use of red coral by the natives of the Malay Archipelago is by Rumphius, who wrote at the end of the seventeenth century. He tells us that the red coral is called by the Malays "Sanhosu," a word which is remarkably like the Chinese "Sanhu" and the Japanese "Sango," and therefore suggests that they

¹ In the *Paulus Aegineta*, published by the Sydenham Society, it is stated on the authority of a Dr. Ainslie that the Tamool practitioners prescribed red coral, when calcined, in cases of diabetes and bleeding piles.

² *Journ. Imp. Fisheries Bureau*, Japan, xiii., 1904.

obtained it originally from China or Japan. Rumphius, however, who insists that it is not found native in Malayan waters, declares that it was brought to the islands by the Portuguese and other Europeans.

There are several later references to the use of coral among the natives of these islands. Valentyn, for example, states that a girdle made partly of glass and partly of gold set with coral was included in the dowry of the daughter of the chief d'Arras of the island of Siauw off N. Celebes in 1677. But in this case, as in others, in which the coral is not more definitely described, it may be doubtful whether it is the red coral of the Mediterranean or some form of black coral.

All that can be said is that it is very improbable that the natives of an island like Siauw, situated in a sea that abounds in coral reefs, would regard black or any form of white coral of such value as to be set as a jewel in a bridal girdle.

Very little is known about the early history of the Malay islands, but the undoubted fact that three centuries ago there was an import of red coral by European merchants lends probability to the view that there was earlier trade in it carried on by the Arabs, who brought with them the beliefs in the efficacy of red coral as a charm and an antidote to poison.

It would be interesting if some definite information could be given as to the routes by which coral was carried in early times from the Mediterranean Sea to the Far East. The discovery of coral in earrings in the Crimea, supposed to be of the fourth century B.C. workmanship, and of the use of coral in inlaid design by the ancient Scythians, suggests that there was an overland route by way of Russia, the Caspian Sea, and Middle Asia.

Pezalotte, who wrote in the early part of the fourteenth century, states that "stript coral, clean and fine coral, middling and small" was sold in the Constantinople market, and it was evidently carried from there by the merchants, who travelled along various routes to the markets of the Far East.¹

¹ H. Yule, *Cathay and the Way thither*, Hakluyt Soc., vol. i., p. 305.

But there seem to have been at least two other routes in early times. In the first century B.C. the Roman navigator Hippalus discovered the sea route from Aden across the Arabian Sea to the markets of India, by which the mercantile ships were able to avoid conflict with the traders from the Persian Gulf. The author of the *Periplus* of the Erythraean Sea, who wrote about A.D. 60, described this new sea route, and told the merchants that there was a demand for coral at Cana (S. Arabia), at Barbaricum (at the mouth of the Indus), at Ozene (=Ujjain on the Malwa coast), and at Bacare (=Porakad on the Malabar coast); and it was probably by this route that a great deal of coral passed by way of the Ganges to Thibet and China.

But the fact that there was already a demand for coral in these places in India at this period of history shows that there must have been an earlier trade in it by another route. This trade was probably conducted by Moors and Arabs from the fisheries of Morocco across Syria, through Mesopotamia, and by way of the river Euphrates to the Persian Gulf.

There are some reasons for believing that in early times the Arab merchants carried on a trade with Africa from Aden by way of an overland route to the Upper Nile, and it is probable that the demand for coral at Cana (in S. Arabia) mentioned in the *Periplus* was to some extent due to its value as an article of trade with negro and negroid inhabitants of that country.¹

The records of the history of the dark-skinned inhabitants of the African continent begin in comparatively modern times, and it is impossible to state even approximately when the negroes first became acquainted with red coral. All that can be said is that, judging from the value they set upon it a few hundred years ago, when the records begin,

¹ It might be expected that the words used by the different races for coral might help in the determination of these trade routes, but so far as I can judge they do not. The following is a list of the names I have been able to collect: *Latin*, Corallium; *Arabic*, Marjan, or a rarer word said to be derived from the *Persian*, Bussadh; *Armenian*, Bust; *Hebrew*, Peninim; *Sanskrit*, Pravala; *Burmese*, Tada; *Thibetan*, Chiru, or, in addressing the higher classes, Guchi; *Chinese*, Shanhu; *Japanese*, Sango; *Malay*, Sanhosu.

it is probable that their trade in coral had a very early origin.

Among the treasures of the kingdom of Benin on the west coast there was found a remarkably fine fly-whisk, composed of several strings of coral beads attached to a handle which is itself a very large solid stem of red coral. From the same and neighbouring states there were obtained some curious network caps strung with coral beads. These specimens may be seen in the British Museum. It is known that there was an extensive trade in coral with Liberia by the Portuguese in the fifteenth century, and these specimens may have come in this way by sea from the Mediterranean.¹

But coral is widely spread among the natives of North Africa and is used partly as an ornament in the form of necklaces of beads, but sometimes as a phallus or in some special form as a protection from the evil eye.² The wandering tribes of Moors carried red coral with them on their travels to "still the tempests and to enable them to cross broad rivers in safety," and probably carried it also as an article of barter with the natives across the desert.

It is impossible to say how long this trade has been going on, but it would be no exaggeration of the facts to say that it began before the Christian era.

Al-Muqadassi, who flourished about A.D. 980, states that the red coral of commerce in his time came from an island named Marsa-al-Kharaz, which was near Bona on the coast of Algeria, and other writers in Arabic, such as Jaqut (1229) and Al-Taifashi (1242), refer to the same island as the principal source of red coral.

There is one great civilisation of North Africa, however, which seems never to have held coral in high esteem, and that is the one of which we have perhaps the most complete records from the earliest times, namely, the Egyptian.³ All through the many dynasties the wealthy Egyptians prided themselves on their necklaces, scarabs, rings, and other kinds

¹ H. Johnson, *Liberia*, vol. i., 1906, p. 74.

² W. Hilton Simpson, *Among the Hill Folk of Algeria*, 1921, p. 79.

³ The predynastic Egyptians used bits of the red Organ-pipe coral (*Tubipora*, p. 116) as beads.

of ornaments of precious stones. They used cornelian, amethyst, garnet, turquoise, lapis-lazuli, and other precious stones, but rarely, if ever, red coral.

We may now consider the evidence of an early trade in red coral in another group of countries. Some years ago a great bronze shield was found in the bed of the river Witham in Lincolnshire which bears five large pieces of red coral, three arranged in a triangle in the centre and two at the sides. Each piece is circular in outline and was ground to form a convex surface and polished. This shield is supposed to belong to the early Iron Age.

Armour decorated with coral in a similar way has also been found in Ireland.

How did the Celts of Britain and Ireland in those early days get their coral to ornament their arms? The answer to this question has been given by Reinach,¹ who traces the trade in coral from the Mediterranean Sea through Gaul to the British Isles. So important does he consider this trade to have been that he speaks of a "coral epoch" in the history of the Ancient Gauls. He tells us it was used for ornamenting weapons of ceremony, shields, armour, fibulae, and other things made of bronze, but rarely used on iron or gold. It was also used as a medicine in various disorders.

This trade in coral, however, came to an end with the Roman Conquest, for the Romans required all the coral they could get for their trade with India by way of Alexandria and the Red Sea as described in the *Periplus*. From that time onwards red enamel seems to have been used by the Celts as a substitute for coral.

It would be interesting to trace the history of the trade in coral from the days of the Roman Empire to the present time, but that is a task that must be left to the patience and skill of the trained historian.

A few words may be said, however, about a series of events in the sixteenth century which heralded an important and critical epoch in the history of the coral fishery.

The later years of the Wars of the Crusaders had brought

¹ S. Reinach, "Le Corail dans l'industrie celtique," *Revue Celtique*, tome xx., 1899.

the European traders into touch with the commerce of the East, and this led to an increased activity and interest in the coral fisheries of the Mediterranean Sea. The Venetians, Genoese, Corsicans, and Moors carried on the trade with the various fluctuations of success that followed their struggles for the supremacy of the sea.

It is probable that the fisheries in shallow water on the north side of the Mediterranean Sea were already showing signs of exhaustion and that envious eyes were cast on the richer coral beds that were known to exist off the coasts of Algeria and Morocco, but the dangers of the voyage across the sea to waters infested with pirates and controlled by a powerful and hostile empire of Mohammedans held in check this source of supply for the Europeans of the North.

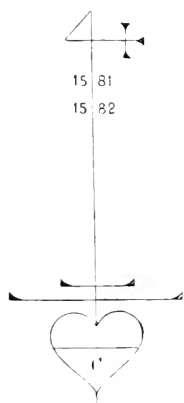


FIG. 110.—Trade mark of the First Coral Company. From Masson.

In the year 1535, however, an alliance was concluded between the French and the Turks with reference to the control of the north coast of Africa, and this was followed by the "Concessions d'Afrique" by which, in 1580, a monopoly of the coral fishery from Cape Roux to La Sebouse was granted by Henri III. of France, with the consent of the Emperor Soliman II., to a French trading company.

The first President of this company was one Thomas Lenche, a Corsican by birth, but a naturalised French citizen of Marseilles. Lenche made a large fortune by his trade in coral, and he was succeeded by his son and his grandson in the business, but in later years international disputes and warfare brought new difficulties and made the monopoly far less profitable.¹

The trade in coral has continued from medieval times with various fluctuations to the present day, although many

¹ The subsequent history of the company and of the battles of the French for the command of the coral fishery on the north coast of Africa is fully related in the works of P. Masson: "Les Compagnies du Corail," *Annales de la Faculté des Lettres d'Aix*, vol. i., 1907; *Histoire des établissements et du commerce français dans l'Afrique barbaresque*, 1903.

of the chief values attributed to coral have become discredited by educated people. Red coral was widely used down to the end of the eighteenth century not only in the form of necklace beads and ornaments but also as a medicine. It was used in the form of a powder and taken in wine or in water for various disorders. John Parkinson, in his *Theatre of the Plants* published in 1640, gives a long list of diseases for which it is commended, such as consumption, the falling sickness, gonorrhoea, sore gums, and ulcers in the mouth. It is also said to cause an easy delivery at birth, and it is much commended "against melancholly and sadness and to refreshen and comfort the fainting spirits."

There are many prescriptions to be found in the pharmacopoeias of the eighteenth century in which red coral is used as an ingredient. The following example of such prescriptions, taken from *A Complete English Dispensatory* by John Quincey, M.D., published in 1739, may be quoted :

It is called *Pulvis purpureus* and is described as a pretty medicine for fevers in children, the measles, and smallpox.

"Take burnt hartshorn, white amber, red coral of each an ounce; crabs' eyes and claws of each two ounces; saffron half a scruple; cochineal two scruples; make them all into a paste, after they are finely levigated with jelly of hartshorn, and form it into little balls which dry and use."

Many other examples could be given to prove the value attributed to red coral for medical purposes in the eighteenth century, but white and black coral were also used although they were not so highly esteemed as the red.

It is quite impossible to say exactly what genera or species of white and of black coral are referred to, but it is certain that the common little alga of our rock pools, *Corallina officinalis*, was used for such purposes (p. 197).

Molière made fun of the practice of giving precious stones as drugs when in *Le Médecin malgré lui* he makes Sganarelle prescribe for a patient "un fromage préparé, où il entre de l'or, du corail et des perles et quantité d'autres choses précieuses." But it was not ridicule that killed the use of coral in medicine, but the spread of knowledge of chemistry and therapeutics. When it was realised that

coral, when analysed, is found to consist of calcium carbonate with traces of calcium sulphate, magnesium sulphate, organic substances, and, in the case of red coral, a trace of oxide of iron, and that its therapeutic value was no greater than powdered chalk, it fell into disuse. In a *Pharmacopœia* of 1677 powdered red and white coral are catalogued; in a *Pharmacopœia* of 1788 red coral only is mentioned; and in Pereira's famous *Materia Medica* of 1842 the only statement that appears is that "coral is still sold in the shops."

Reference has been made to the use of red coral by natives of North Africa as a phallus and as a protection against the evil eye. It is said to be used for the same purposes by the peasants of Italy and of other parts of South Europe. The superstition that seems to have been most persistent in this country is that it assists children in the cutting of their teeth.

"It helpeth children to breed their teeth, their gums being rubbed therewith; and to that purpose they have it fasten at the ends of their mantles."—Coles in *Adam and Eden*, quoted by Brand.

Fabritio. Art thou not breeding teeth. . . . I'll be thy nurse and get a coral for thee and a fine ring of bells.—BEAUMONT AND FLETCHER, *The Captain*, Act iii. sc. 5 (ca. 1613).

From this superstition, undoubtedly of Roman origin, is probably derived the custom still prevalent in many families in this country of decorating their young children with a necklace of coral beads.

And thus there survives to the present day the last relic of the virtues conferred upon coral by Minerva to commemorate the victory of her brother Perseus over the Medusa.

BLACK CORAL

It has already been stated that according to some commentators the Arabic word Ramoth, translated "coral" in the English Version of the Bible, probably meant "black coral." There seems to be no doubt that some kind of black

horny axis of a marine organism was used, from very early times, as an ornament or as a talisman on account of the magical properties attributed to it.

The ἀντιπαθής of the ancient Greeks was, in all probability, a kind of black coral, and was considered to be of value as an antidote to the stings of scorpions and for other medical and magical purposes.

According to some of the older writers the herb given by Mercury to Ulysses as a charm to protect him from Circe was a piece of Antipathes. Rumphius quotes Salmasius as having written in his notes on Solinus that Antipathes was used as a protection against sorcery. Pliny refers to it in his alphabetical list of stones. He says, Book xxxvii. chap. 54, "Antipathes is black and not transparent: the mode of testing for it is by boiling it in milk to which, if genuine, it imparts an odour (?) like that of myrrh. The magicians also assert that it possesses the power of counteracting fascinations." Dioscorides regarded Antipathes as a kind of black coral which was possessed of certain medical properties. The substance called Charitoblepharon, mentioned by Pliny (*Nat. Hist.* xiii. 52), which was said to be particularly efficacious as a love charm and to have been made into bracelets and amulets, was probably some kind of black coral.

These and other vague references to the substance by ancient Greek and Roman authors do not, it is true, give us any certain clue as to the identity of their Antipathes, and it is only by indirect circumstantial evidence that the conclusion is arrived at that it was the axis of one of two or three kinds of marine flexible corals.

The word Antipathes has been handed down to us from the Greeks, by the Roman writers Pliny and Solinus, and by the naturalists of the sixteenth and seventeenth centuries as the name of one of the flexible corals with a black horny axis. In modern systematic zoology it is the name of one genus of the Antipatharia. It does not follow, however, that what we call Antipathes to-day is the same thing as the Antipathes of the Greeks and Romans. In fact, it is almost certain that the ancient writers would have

called anything of the nature of a black horny axis Antipathes, whether it was Antipathes, Gerardia, Plexaura, or Gorgonia.

Pliny's milk test for Antipathes is interesting but unfortunately very obscure. The phrase he uses is "experimentum eius, ut coquatur in lacte ; facit enim id murrae simile." But similar to myrrh in what respect ? In odour, in colour, or in form ? Solinus considers it to have been similar to myrrh in odour (*Collect.* v. 26), but other authors have interpreted Pliny to mean similar to myrrh in colour. If this test be applied to a piece of Antipathes it will be found, after prolonged boiling in milk, to have a faint odour resembling that of heated myrrh, but the colour of neither the milk nor the coral seems to be in any way affected. For this reason it seems probable that Pliny meant to say "similar in odour to myrrh."

In modern times black coral is still in use in the form of bracelets worn on the wrist or arm as a cure for rheumatism, as a protection from drowning, and for other purposes of a similar kind. Bracelets and other articles of the same material are worn in China and Japan, in the Malay Archipelago, and in the islands of the Indian Ocean ; and there is reason to believe that the belief in its virtues has been handed down by tradition from very ancient times.

In his book on the *Antiquities of the Jews* (i. 3. 6), Josephus relates that according to Berosus, the Chaldean, there is still some part of Noah's Ark in Armenia, and the natives carry off pieces of the bitumen (pitch ?) to make into amulets for averting mischief. We have in this passage reference to a substance like bitumen (*i.e.* black and flexible when heated) which was believed to possess magical properties. Of course, it may not have been black coral at all, but if black coral accompanied by the beliefs in its efficacy against evils of many kinds was transported to distant parts of the world, as we know red coral was transported at that period, it would not be remarkable if it became associated with the Noah's Ark myth.

It would be a matter of great interest if scholars learned

in Jewish antiquities could throw any further light on the use of either black or red coral by the Children of Israel in early times.

The most complete account of this superstition in the Malay Archipelago is to be found in Rumphius's *Amboinsch Kruidboek*, xii. p. 195, published in 1750, in the article on *Corallium nigrum* or *Accarbaar itam*. He says that the natives make bracelets of it by soaking it in cocoanut oil and bending it into the form required over a slow fire while smearing it all the time with oil. It is then polished with a rough leaf. Sometimes it is inlaid with gold or silver ornaments. It is sometimes made into sceptres for the chiefs, and it is also made into a powder by grinding with a stone, mixed with water and drunk as a medicine. It would take too much space to give in detail the various diseases for which black coral was used as a remedy ; but it is evident that its virtue was not supposed to be confined to the cure of rheumatism and other diseases, as it was used for ensuring the healthy growth of children, and by adults for protection against sorcery, and by the great chiefs as a symbol of dignity or power.

There were other kinds of Accarbaar or Bastard corals which were known to the Malays in the time of Rumphius and used by them for medicinal purposes, but the *Accarbaar itam* or *Corallium nigrum* was regarded as the most important and was held in the highest esteem. Among these was the *Accarbaar puti*, which, from the figure given by Rumphius, was an Alcyonarian belonging to the family Isidae and probably to the type genus *Isis*. This is of some special interest, as the Mediterranean species of *Isis* was held in high esteem by the Mediterranean races in classical times and was currently believed to represent the petrified hair of Isis. But that is another story, and one about which only the most fragmentary indications remain.

The task of identifying the various kinds of black coral mentioned by the ancient and subsequent writers up to the end of the eighteenth century is an extremely difficult one, as detailed descriptions of the characters upon which the modern classification is based are almost entirely lacking.

The substance was evidently black or dark brown in colour ; it was capable of being bent or twisted when subjected to heat and it was hard enough to be given a polished surface. Moreover, it may be presumed from various references that it was a product of the sea.

It might therefore have been the Keratin axis of one of the Plexauridae, of one of the Gorgonidae, or of one of the Antipatharia, or finally of *Gerardia savalia*.

The *Accarbaar itam* of Rumphius was probably a Plexaurid. The figure of the stript coral that Rumphius gives is not conclusive, but quite consistent with this identification. In the description of the coenenchym, which covers the axis when it is fresh, he uses the Dutch word "Schorse," *i.e.* bark, whereas in the description of another Accarbaar, which is almost certainly a Gorgonid, he uses the word "Korste," *i.e.* crust. In the description of a third Accarbaar, which is obviously an Antipatharian, he uses the word "Slijm," *i.e.* mucus. With such an accurate observer as Rumphius was, we may assume that the use of these different words for the coenenchym signified a real difference in character between them. In the Plexauridae the coenenchym is relatively thick, in the Gorgonidae it is almost invariably thinner, whereas in the Antipatharian it is usually little more than a soft and delicate covering of the axis.

Rumphius states that the *Accarbaar itam* is not identical with Pliny's Antipathes because it does not give the smell or colour of myrrh on boiling in milk. For other reasons than this, however, we may feel certain that the Antipathes of Pliny and the earlier writers was not a Plexaurid. The evidence seems to point to the conclusion that the black coral commonly used by the ancients was the form mentioned by Imperato (1599) as Savaglia and now known as *Gerardia savalia*. (Until quite recently *Gerardia* was considered to be an Antipatharian, but it has now been definitely placed in the order Zoanthidea.) The reason for believing that it was *Gerardia* is that this coral grows in the Mediterranean Sea, whilst the Plexauridae do not, that it attains to great dimensions (a great specimen in the British Museum being

two metres in height and spreading fan-wise to a width of over two metres), and the surface of the branches is smooth and devoid of spines. It is possible that in addition to the *Gerardia* the main stem of some of the species of *Antipatharia* that are found in the Mediterranean Sea may also have been used. Gansius in his *Historia coralliorum* (1666) describes a species, *Antipathes hirsutum*, found in the Sardinian Seas, which is in length greater than the human stature. The axis of such a specimen if polished would be difficult to distinguish from that of *Gerardia*.

The difficulty of determining the black coral of the ancients, however, is due to the possibility that they may have imported it from the South, in which case Plexaurid or Gorgonid coral may also have come into use. Thus Pliny says in writing on coral, *Nat. Hist.* xxxii. 11, "gignitur et in Rubro quidem mari sed nigrius item in Persico—vocatur Iace—laudatissimum (*i.e.* red coral) in Gallico sinu circa Stoechades insulas, etc." This passage indicates that the most valuable kind of coral known to the Romans came from the Isles D'Hyères and other places in the Mediterranean Sea, but a black kind was also imported from the Red Sea and the Persian Gulf in which the *Corallium nobile* is not found.

Black coral was also known to the Moors in early times, and was very probably obtained by the fishermen engaged in the famous red coral fishery off Marsa-al-Kharaz, the modern Bona or Bône on the coast of Algeria. The Arabic name for black coral was "yasz" or "yusz," a word which seems to have some resemblance to Pliny's word "jace."

These few notes on the use of black coral in early times may seem to be very fragmentary and inconclusive, but they may be perhaps sufficient to create some interest in and to stimulate further investigation in a chapter of zoological mythology which has not yet been written. It is probable that classical and Oriental research will reveal a great many more references to this substance than are recorded in these notes, and it may be expected that the excavations of the antiquaries will bring to our collections some specimens of

black coral that were used in ancient times ; but there is sufficient evidence to prove that the belief in the magical properties of black coral is not only widespread at the present day, but carries with it the sanction of a tradition which has been transmitted from the early days of our Western civilisation.



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